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AGGRESSIVE BEHAVIOURS OF TERRITORIAL CICHLID FISHES AGAINST LARGER HETEROSPECIFIC INTRUDERS

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ABSTRACT Aggressive behaviours at nesting territories of cichlid fishes were observed in Lake Tanganyika. Subject fishes were *Neolamprologus toae, Tropheus moorii, Ophthalmotilapia nasutus, Limnotilapia dardennii* and *Petrochromis polyodon*. They attacked and repelled various sized heterospecific fishes from the territories. Against much larger intruders, the fishes quickly approached and pecked them. The larger fishes never conducted counter-attack, and left the territories. Such pecking behaviour was regarded as a kind of attack, but greatly different from attacks in interspecific territorialities of cichlids reported hitherto, which are usually organized in size-dependent dominance relationships. This paper discusses the domination of the nesting territory owners in a context of 'symmetry' of territoriality.

Key Words: Territorial behaviour; Domination; Nesting territory; Territorial mosaic.

INTRODUCTION

Tropical waters usually include large numbers of fish species. In such habitats, fishes develop a variety of interspecific relationships (Lowe-McConnell, 1987; Hori, 1987, 1991; Kohda, 1991a, 1991b), among which interspecific territoriality is common and has been studied by many authors (Miller, 1978; Kohda, 1993). Interspecific feeding territories of herbivorous damselfishes or cichlid fishes, as well as intraspecific ones, are arranged in a territorial mosaic (Keenleyside, 1979) and are usually organized by size-dependent dominance relationships (Myrberg, 1972; Keenleyside, 1979; Kohda, 1991, 1993; Kohda & Yanagisawa, 1992), where larger territory owners attack neighbours and smaller fish carry out appeasement display towards neighbours (Kohda, 1991a, 1993; Kohda & Yanagisawa, 1992).

Many cichlid fishes maintain nesting territories, which are usually small, 1–2 m in diameter, and are defended against various kinds of fishes, most of which are potential brood predators (Kohda, 1991, 1993). During our field study, we observed that some cichlids with nesting territories attacked larger heterospecific intruders as well as smaller ones. The purpose of the present paper is to understand the dominance against larger fishes. We will describe aggressive behaviour at nesting territories of five Tanganyikan cichlid fishes, and discuss their dominance over much larger fishes, in comparison with the size-dependent dominance order in the cichlids' territorialities reported before. In repelling much larger fishes, nest ter-

ritory owners pushed much larger intruder with their heads, described as pecking behaviour below. This behaviour is noteworthy, because a similar behaviour reported in one of the 5 cichlids has been regarded as non-aggressive.

STUDY SITE AND METHODS

Field observations were conducted at Bemba, about 25 km south of Uvira (3° 24' S, 29° 10' E), Zaire, during January to April 1989, with the aid of scuba equipment. A 20m × 20m quadrat was set up on a rocky and sandy bottom in which 34 cichlid fish species dwelt.

Subject species were five cichlids abundant in the study area; *Neolamprologus toae, Ophthalmotilapia nasutus, Tropheus moorii, Limnotilapia dardennii* and *Petrochromis polyodon. Petrochromis polyodon* was also observed on the rocky shore of Kasenga Point at the southern end of this lake, September to November 1992. They maintatin territories around the nest or spawning sites from which various fishes are repelled (Nakano & Nagoshi, 1990; Kohda, 1993). Most intruding fishes were potential egg or brood predators. *Neolamprologus toae* is a substratum brooder and a shrimp eater. The others are maternal mouthbrooders and herbivorous (Kuwamura, 1986). Both parents of *N. toae* defend a nest site with eggs or juveniles (Nakano & Nagoshi, 1990), and males of the other four species defend the spawning sites (Kohda, 1993). In this paper, both territories will be called nesting territory. *Tropheus moorii* and *P. polyodon* maintain much larger feeding territories (against congeneric fishes) (3–6 m in diameter) in which the nesting territories are located (Kohda, 1991, 1993).

Prior to the present study, we noticed that some territory owners conducted a pecking behaviour against heterospecifics, similar to that reported in *T. moorii* (12 cm) against *P. polyodon* (22 cm) (Takamura, 1984). The sequence of such pecking behaviour was as follows: when much larger fishes approached a nesting territory, the territory owner quickly approached or dashed into and banged on their opponents' lateral side and pushed them. In normal attacks against heterospecifics, the territory owners attacked and chased fleeing intruders, and, consequently, they rarely came in contact. However, the pecking behaviour included direct contact.

The other territorial behaviours between heterospecific cichlid fishes reported before are lateral displays (Kawanabe, 1981; Kohda, 1991, 1993; Kohda & Yanagisawa, 1992), conducted by smaller territory owners against larger neighbours near territory borders. The territory owner shows its lateral side in a variety of angles to the opponents and quiver their fins and bodies more or less violently. The two participants rarely made contact. Thus, this behaviour is different from the pecking behaviour.

Observations on nesting territories were conducted among three pairs of *N. toae*, five males of *T. moorii*, five of *O. nasutus*, and six of *L. dardennii* and three of *P. polyodon*. Topographical maps (1/20) of each nest or spawning site were prepared, on which points of attack against intruders, their species names, total length of attacked fishes at the territories were recorded for 3–5 hours in total for each species. Total length of the territory owner and each intruding fish was estimated to

Table 1. Attacks (A) and pecking behaviours (P) by owners of nesting territories of *Neolamprologus toae*, *Tropheus moorii*, *Ophthalmotilapia nasutus*, *Limnotilapia dardennii* and *Petrochromis polyodon*. Figures in parenthesis indicate total length (cm).

Attacked fishes	*N. toae* (6–7)		*T. moorii* (11–12)		*O. nasutus* (10–11)		*L. dardennii* (20)		*P. polyodon* (21–22)	
	A	P	A	P	A	P	A	P	A	P
Herbivores										
Cyathopharynx furcifer	0	0	0	0	2(12)	0	1(12)	0	0	0
Eretomodus cyanostictus	0	0	0	0	0	0	0	0	3(5–6)	0
Limnotilapia dardennii	0	0	0	0	0	0	0	0	3(8–24)	0
Ophthalmotilapia nasutus	0	0	0	0	0	0	5(10–11)	0	0	0
O. ventralis	0	0	0	0	0	0	0	0	7(8–10)	0
Petrochromis famula	0	0	0	0	0	0	5(11–13)	0	0	0
P. fasciolatus	0	3(18)	0	0	1(15)	0	3(13–16)	0	3(10–12)	0
P. orthognathus	1(10)	0	0	0	0	0	2(14–16)	0	0	0
P. polyodon	0	1(19)	0	0	0	3(19)	3(17–18)	0	0	0
P. trewavasae	2(11)	2(17–18)	1(8)	0	0	0	9(11–18)	0	0	0
T. duboisi	0	0	0	0	0	0	1(8)	0	0	0
Tropheus moorii	0	1(12)	1	0	1(11)	0	5(10–12)	0	14(10–12)	0
Omnivores										
Neolamprologus moorii	0	0	0	0	0	0	0	0	21(5–10)	0
Telmatochromis temporalis	5(5)	0	13(4–6)	0	12(4–5)	0	9(4–5)	0	0	0
T. bifrenatus	0	0	0	0	5(4–5)	0	1(5)	0	2(5–7)	0
T. vittatus	0	0	0	0	0	0	0	0	2(5–6)	0
Carnivores										
Altolamprologus compressiceps	0	0	3(5–6)	0	0	0	0	0	0	0
Julidochromis marlieri	1(5)	0	3(5–6)	0	7(5–6)	0	3(6–8)	0	0	0
*Mastacembelus spp**	0	0	1(?)	0	0	0	1(15)	0	3(10–25)	0
*Lamprichthys tanganicanus**	0	0	0	0	0	0	2(10)	0	3(8–14)	0
Lepidiolamprologus elongatus	1(8)	0	2(8–10)	0	0	0	8(7–9)	0	1(12)	0
L. profundicola	5(7–8)	0	0	0	1(10)	0	1(12)	0	0	0
Lobochilotes labiatus	0	0	0	6(24–30)	0	1(30)	0	0	4(8–20)	3(25–35)
Neolamprologus bricharid	9(5–6)	0	4(5–6)	0	5(5–6)	0	19(5–7)	0	8(6–8)	0
N. mondabu	3(4–6)	0	1(8)	0	2(7)	0	3(5–7)	0	0	0
N. savoryi	0	0	1(5)	0	0	0	0	0	0	0
N. toae	0	0	0	0	1(7)	0	2(7)	0	0	0
N. tretocephalus	1(10)	0	0	0	0	0	0	0	0	0
Total	28 (5–11)	7 (12–19)	30 (4–10)	6 (24–30)	37 (4–15)	4 (19–30)	83 (4–18)	0	74 (5–25)	3 (25–35)

Food habits are cited from Takamura, 1984; Hori, 1987; Kohda & Hori, 1993 and Hori, unpublished data.
*: Non-cichlids.

the nearest 1 cm by comparing them with rulers placed near the territories. In general observations in the study area, if the pecking behaviour was observed, the participant species names, their body sizes and the sites were recorded.

RESULTS

Observed fishes chased away various kinds of heterospecific intruders (a total of 28 species) from their nesting territories (Table 1). They attacked intruding fishes smaller than or slightly larger than each territory owner, irrespective of the food habits (Table 1). Appeasement displays of the territory owners toward approaching heterospecifics were never observed.

A total of 20 pecking behaviours was observed among small *N. toae*, middle-sized *T. moorii, O. nasutus* and large *P. polyodon* (Table 1). The behavioural patterns were similar among them. The pecking behaviour occurred on the borders of nesting territories of the four species, and were never observed outside nesting territories. This behaviour was directed to much larger intruders (Table 1), who never conducted counter-attacked against the territory owners, and left the territories.

The smallest *N. toae* and middle-sized *O. nasutus* carried out pecking behaviour against fishes of *Petrochromis* ranging from 17–19 cm in size. But *Petrochromis* fishes of this size were attacked by the large-sized *P. polyodon* and *L. dardennii* (Table 1).

The body size of two species of intruding cichlids ranged widely: *Petrochromis trewavasae* from 11–18 cm, and *Lobochilotes labiatus* from 6–35 cm. *Neolamprologus toae* attacked the smaller (11 cm) *P. trewavasae*, but showed pecking behaviour against the large ones (17–18 cm). *Petrochromis polyodon* attacked smaller *L. labiatus*, but performed pecking behaviour against larger fish (Table 1). These results suggest that the territory owners alternate attacks and pecking behaviours according to the size of the intruders. We concluded that the pecking behaviour is conducted by the nesting territory owners against much larger intruders.

DISCUSSION

Interspecific interactions where one fish attached its mouth to the other's lateral side is rare except in cleaning. In the pecking behaviour, the defender attached its head to the lateral side of larger heterospecific fishes. However, considering (1) the rapid dash without examination of the body surface of the larger intruder, (2) the location where this behaviour occurs and (3) the mouth shape of the four cichlids (Poll, 1956), it was implausible that this behaviour was body cleaning.

The pecking behaviour in four species could be seen as one of territorial behaviour against much larger intruders, and were effective in repelling them. The territory owners were dominant over even much larger heterospecific fishes in the territories. Indeed, no appeasement behaviour toward larger intruders were observed.

Feeding territories of herbivorous Tanganyikan cichlids, such as *Petrochromis*

and *Tropheus* (ca. 3–6 m in diameter), are arranged in a territorial mosaic and were each defended against mainly conspecific and congeneric neighbours (Takamura, 1984; Kohda, 1991, 1993; Kohda & Yanagisawa, 1992). All the individuals are organized by intra- and interspecific size-dependent dominance orders: the larger fishes attack territorial neighbours and the smaller one conducted appeasement displays (Kohda, 1991; Kohda & Yanagisawa, 1992). In this form of territoriality, smaller fish cannot maintain territories against much larger neighbours more than twice their size (Kohda, 1991).

The nesting territories of the five cichlids are narrow, about 1 m in diameter. In contrast, the larger heterospecific intruders into the nesting territories have usually much larger home ranges or territories (Takamura, 1984; Kohda, 1991, 1993, in press). For such larger intruders, the narrow territories of the cichlids were too tiny to expend their energy in repelling them. On the other hand, these small areas were indispensable for the cichlids as their territory. Thus, the value of the small area depended on the participants of the conflict and, consequently, their aggressiveness depended on motivation.

In contrast, adjacent feeding territories of herbivorous cichlids, *Tropheus* or *Petrochromis* had similar sizes regardless of species (Takamura, 1984; Kohda, 1991, 1993; Kohda & Yanagisawa, 1992). In other words, they partition a rocky bottom, a foraging site, so that the areas were equal.

The herbivorous damselfish, *Stegastes altus* maintains a feeding territory (3–4 m in diameter) from which much larger heterospecific food competitors (more than twice in size) were one-sidedly attacked and repelled. All the competitors are wandering fish species with much wider home ranges (Kohda, 1981, 1984, 1989). Such dominance of feeding territory owners against much larger heterospecific intruders has also been reported in other damselfishes, *Pomacentrus flavicauda* (Low, 1971) and *Stegastes leucostictus* (Ebersole, 1977). Dominance against wandering competitors seems analogous to that of nesting territories in the present study. However, some territorial damselfishes that maintain a territorial mosaic and share substrata are organized in a size-dependent dominance order (Myrberg, 1972; Kohda, personal observations). In general, fishes in a territorial mosaic are usually organized in size-dependent dominance order, but in an 'asymmetric' situation, territory owners could dominate larger fishes with much wider home ranges.

Although many studies on interspecific territorialities have been conducted, most were concerned with territories arranged in a territorial mosaic (Orians & Wilson, 1964; Murry, 1981; Ydenberg et al., 1988). Highly diversified fish communities, such as those in coral reefs or tropical lakes, generate complicated interspecific relationship (Hori, 1987, 1991; Kohda, 1993). Studies on various forms of interspecific territoriality in such communities will help to understand territoriality itself.

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