HEAD RAMMING BEHAVIOUR BY THREE PAEDOPHAGOUS CICHLIDS IN LAKE MALAWI, AFRICA

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Abstract. We observed three cichlid species, Cynotoca orthognathus, C. lieni and an undescribed species, feeding on eggs, embryos and larval stages of mouthbrooding cichlids in Lake Malawi. Each species engages in a unique head ramming behaviour, forcing females to jettison some young involuntarily. The three paedophagous species had either eggs, embryos and/or larval fish in their stomachs. Cynotoca orthognathus mimicked females by turning on and off its stripe depending on whether or not it was stalking the silver C. eucinotomus or the striped C. pleurotaenia. We discuss two previous hypotheses concerning how paedophages capture their prey and conclude that ramming of females is the manner by which most paedophages obtain their food in nature.

Cichlid fishes have evolved a great diversity of feeding adaptations enabling them to exploit a wide variety of food including phytoplankton, zooplankton, detritus, epilithic and epiphytic algae, higher plants, molluscs, insects, benthic crustaceans, fish parasites, whole fish, fish scales and fins, fish eggs, fish embryos, and fish larvae (Fryer & Iles 1972). The existence of paedophagous fishes that primarily exploit fish embryos and larvae, was first reported for the Lake Victoria cichlid flock (Greenwood 1959, 1967, 1974). These reports were based on stomach analyses.

A controversy exists over the mechanism by which these paedophagous cichlids capture embryos and larvae. Greenwood (1959) hypothesizes that a paedophagy engulfs the snout of a mouthbrooding cichlid female causing her to disgorge her brood. Fryer & Iles (1972), however, contend that females voluntarily jettison their young under stressful conditions and that the young are then eaten by a paedophage. They propose that such behaviour is a mechanism enabling cichlid populations to regulate their own densities.

Support for Greenwood's snout-engulfing hypothesis was provided by observations in an aquarium of Haplochromis parvidens. The observations showed 'buxuous patterns that suggested that H. parvidens engulf the snout of a brooding female' (Greenwood 1974). Furthermore Wilhelm (1980) observed an individual of an undescribed Lake Victoria cichlid engulfing the snout of a brooding female. Observations supporting the voluntary jettisoning hypothesis have been made by an aquarist. K. Speen observed that Pseudotropheus zebra, P. auratus and Labeotrophaeus trewavasae from Lake Malawi jettison their broods voluntarily in aquaria (Fryer & Iles 1972).

There have been, however, no field studies of paedophagous behaviour prior to this report. We observed three cichlid species, Cynotoca orthognathus (Fig. 1, Plate I), C. lieni (Fig. 2, Plate II) and an undescribed cichlid (Fig. 3, Plate I) in Lake Malawi 'ram' brooding female cichlids and remove young from their mouths. We suggest here that such ramming is probably the most common method of extracting eggs, embryos or larvae from a female cichlid's mouth in Lake Malawi.

Methods

Three paedophagous species were studied at an area 50-150 m south of Outer Point, Lake Malawi (34° 49' E, 14° 03' S). A permanent 0.5 hectare grid was marked out with lines. The study site was an area of sand, surrounded by rocks, at a depth of 7-11 m. This grid was established to study a multispecies cichlid breeding area that included Cynotoca eucinotomus, C. pleurotaenia, Lethrinops liturus, L. aarti and L. sp. Males of these species build nests which they vigorously defend and in which they court females. Above the arena are large schools of fish composed primarily of females of these five species. It was here that we first observed paedophagous predation by cichlids.

Observations on the feeding behaviour of C. orthognathus, C. lieni and the undescribed species were made in July 1979 and in June through August 1980. All observations were made underwater by divers using SCUBA. Individuals of each species were observed for 15
min at an average distance of 2.5 m. Twenty-two individual observations were made on C. orthognathus and 8 on C. lieni. The undescribed cichlid was rare, consequently qualitative observation, 35 mm slides, and 8 mm movies of 3 individuals were used for a total observational period of approximately two hours. The data collected included the number of times C. orthognathus and C. lieni rammed into females, and the number of times these species were attacked or threatened by territorial males of C. eucinostomus, C. pleurostoma, L. aurita, L. littorai and L. sp.

We counted all individual predatory species within 3 m on either side of four 75 m transects every 3–11 days from June 6 to August 23, 1980 (N = 28) to determine fish densities.

Stomach analyses were conducted on fish that had either been chased into block nets by SCUBA divers or captured in trammel nets that had been set overnight. No predatory fish were removed from the study area while the observations were being conducted.

**Results**

**Densities**

_Cryptocara orthognathus_ was the most common predatory species observed in the study site, but even this species occurred at the low density of 1.0 per 2800 m², or approximately 0.02 for the study grid (range 0–4). Only one _C. lieni_ was counted on the 28 transects. We never observed, while making behavioral observations, more than two _C. lieni_ at one time and they were often unsuccessful in finding them on the grid. The undescribed cichlid was observed only twice at the deeper parts of the grid.

**Stomach analysis**

Eight of the 14 _C. orthognathus_ stomachs examined contained eggs and embryos; the other six fishes, all of which were gravid females, had empty stomachs. Two of the four _C. lieni_ stomachs examined contained larval fish (5–8 mm Total Length (TL)). A third stomach contained eggs and the fourth was empty. The one stomach of the undescribed species examined contained 7 larval fish between 6 and 9 mm TL.

**Behaviour of _C. orthognathus***

The only observation of feeding behaviour by _C. orthognathus_, was ramming of females to remove young from their mouths. During a 15 min watch intervals usually covered an area of 500–1500 m² as estimated by a minimum rectangle (Barlow 1975). As _C. orthognathus_ swam along the bottom it was subjected to frequent attacks from territorial males (Table I). The closer to the bottom it was, the more attacks _C. orthognathus_ drew from territorial males. _Cryptocara orthognathus_ was usually observed swimming 1–2 m above the sand of the grid.

The principal method of hunting was to stalk brooding females in the water column. These females were easy to distinguish because of the distension of their opercula caused by the off-spring in their mouths. _Cryptocara orthognathus_ slowly approached a female from underneath and behind, swimming until it was underneath the belly of the brooding female approximately 1–2 fish lengths behind and 45° below. The predatory then darted up, rammed the female in the hyoid region. If _C. orthognathus_ had caught the brooding female by surprise it continued past the female's mouth and began chewing motions. If the female turned, causing the predatory to miss on the first dart, the predatory moved on. Because the action happened so fast, the mechanism by which the predatory gets the young out of the female's mouth is still unclear. It appeared, however, that

<table>
<thead>
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<th>Table I: Interactions between Prey and their Target Species</th>
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<tr>
<td>Mean number of females rammed per hour</td>
</tr>
<tr>
<td>(N)</td>
</tr>
<tr>
<td>C. orthognathus</td>
</tr>
<tr>
<td>C. lieni</td>
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<tr>
<td>Mean number of attacks and threats from territorial males per hour</td>
</tr>
<tr>
<td><em>C. eucinostomus</em></td>
</tr>
<tr>
<td>C. orthognathus</td>
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<tr>
<td>C. lieni</td>
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the impact forced the mouth to protrude, involuntarily ejecting the young into the path of the pseudophagia.

C. orthognathus concentrated its attacks primarily upon two species: C. eucinostomus and C. pleurotaenia (Table 1). Usually C. orthognathus appeared grey with an oblique stripe, but when stalking C. eucinostomus its stripe disappeared and the fish became bright silver. However, when stalking C. pleurotaenia the stripe reappeared (Fig. 1, Plate I). The colour pattern of the pseudophagia closely matched that of the fish being stalked. During a 15 min observation the stripe appeared and disappeared as many as eight times. It took between 10 and 15 s for the stripe to modulate.

Behaviour of C. lieni

The hunting behaviour of C. lieni differed slightly from that of C. orthognathus. Instead of approaching from behind and slightly below the female, this species attacked from 0.5 to 2 m below the female at a 70-90° angle (Fig. 2, Plate II). The attack was directed at the same region of the female's head. We only observed C. lieni ram C. eucinostomus. C. orthognathus lieni was subjected to significantly fewer attacks by both male C. eucinostomus (Mann–Whitney U, \( p < 0.05 \)) and C. pleurotaenia (Mann–Whitney U, \( p < 0.01 \)) than was C. orthognathus. During the two hours of observations, C. lieni was attacked once by male C. pleurotaenia (Table 1).

Behaviour of The Undescribed Cichlid

The third species was rare both in the study area and throughout the Cape Natural region (see Fig. 1, McKay 1981) where the trammel nets were set to collect fish for a general faunal survey (field data and specimens to be deposited in the National Museum, Washington, D.C.). One individual was first observed at 14 m in the deep portion of our grid. We made subsequent 8 mm movies of three individuals at 13-20 m depths outside the main study area. These individuals were from 160 and 160 mm standard length. They were considerably larger than the average C. orthognathus and C. lieni (average 114 mm SL and 110 mm SL respectively).

The undescribed cichlid directed all of its 20 attacks against C. pleurotaenia females (130-150 mm SL). During these observations we never saw the undescribed cichlid attack the smaller (70-90 mm SL) C. eucinostomus females that were present.

There was a marked difference in the attack mode of the undescribed cichlid from that of C. orthognathus and C. lieni. The undescribed cichlid attacked from above and hit the C. pleurotaenia females on the snout near the premaxillary pedicle. Interestingly this undescribed cichlid only received attacks from territorial C. pleurotaenia males. During 2 h of observations we never saw the pseudophagia attacked by C. eucinostomus.

Response of Brooding Female

Often the female noticed the pseudophagia immediately before the attack; she then circled quickly 180° to a position behind the pseudophagia. If the female noticed the approach earlier she turned on her side or darted off. The pseudophagia did not chase these females farther.

Aggression Between Pseudophages

Aggressive interactions between pseudophages were relatively rare because pseudophagia density was low. However, when pseudophages encountered one another, attacks were severe. The winner often chased and repeatedly attacked the loser for a distance of 20-30 m. During 7 h of observations upon these fish, we saw six pseudophagia attack on other pseudophages.

Discussion

Cichlid fishes have evolved a broad array of behavioural adaptations for exploiting various foods. Some of the behaviour employed by cichlids such as playing dead to capture food (Fryer 1956; McKay 1981), appears to be unique to the family. Similarly, ramming behaviour as reported here has never been recorded in non-cichlids.

Although the three pseudophages share the behaviour of ramming the heads of brooding females, they each employ a different method. The variations in the attack pattern of the pseudophages may make it difficult for females to develop effective countermeasures against attack. Furthermore, the most common pseudophagia, C. orthognathus, changes its colour to mimic the silvery C. eucinostomus or the striped C. pleurotaenia. These different methods of utilizing the same food resource together with the facultative ability to mimic the prey by one species probably contribute to the ability of the three species to coexist.

The three species nevertheless are rare and the density of brooding females is three to four
orders of magnitude greater than that of the paedophages. Why then aren't there higher densities of paedophages to exploit this potentially underutilized resource? Three factors probably account for the low numbers of paedophages: (1) a density-dependent female response to their presence, (2) aggression between paedophages, and (3) attacks upon them by territorial males of the species they are exploiting.

Females avoided the paedophage the longer it remained in a localized area within the school. After about 1–2 min the paedophage moved about 5–25 m before hunting again among a new group of females. As one paedophage species increases in numbers we predict that females will become more wary of that species and its success rate will decline. Even C. orthognathus, which facultatively mimics two species and hence can move closer to its prey before attacking, should occur at a low density. Theory predicts that for the relationship to continue, the mimic/model ratio should be low (Wickler 1968).

The aggressive interactions between paedophages and the driving away of intruding conspecific and interspecific paedophages may restrict the number of paedophages in a localized area. An additional challenge for the paedophage is the continual attack by territorial males. These attacks make it difficult for the paedophage to approach the brooding females successfully. Territorial males appear to concentrate their attacks upon the paedophages that are a threat to conspecific females (Table I). C. ortognathus, which switched between species of brooding females, was attacked frequently by both C. eucinostomus and C. pleurotaenia males. C. ortognathus males were undescibed species was attack by C. pleurotaenia males (see Table I for summary).

Overview of Paedophagy by Cichlids

1. Voluntary jettisoning of young. Egg-eating and the devouring of free swimming fry by cichlid fishes has been observed numerous times during the course of our studies at Lake Malawi, Africa (McKaye & Oliver 1980) and Lake Jiloa, Nicaragua (McKaye et al. 1977a, b; McKaye & McKaye 1977). We have not seen, however, an unprovoked jettisoning of a brood, as suggested by Fryer & Iles (1972).

The conditions under which a female should voluntarily sacrifice her young are rare. Abandonment would be predicted only when the anticipated costs per offspring required to take care of the remaining young were greater than those associated with starting over again with a larger brood (Dawkins & Carlisle 1976). These conditions would most likely be met if (1) the brood decreased to such a size that energetically the costs would be less to yolk up more eggs and start over again with a full sized brood or (2) the female was in such jeopardy that caring for the young threatened her existence and ability to reproduce again. Fryer & Iles (1972) suggest that a female who has passed through a period of food scarcity would jettison her eggs. However, such a case is not likely to satisfy either of the previous two conditions. The future reproductive value of an offspring increases with age. The cost of sacrificing young, in terms of future parental investments, generally increases with age and state of development (Trewers 1972). Therefore a female probably would postpone breeding until she had built up sufficient fat reserves rather than going to the energetic expense of producing, laying and then jettisoning them voluntarily.

2. Snout engulfing and ramming of females. Never having seen snout-engulfing in nature, we suggest that it is not the prevalent manner in which cichlids obtain young from brooding females. Snout-engulfing is hypothesized to have evolved from mouth-fighting (Wilhelm 1980), but there is a critical difference between two behaviours. In snout-engulfing, one fish tries to flee from the other, whereas in mouth-fighting both

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Table II. Summary of Species Interaction; + Common, – Rare or Never Seen

<table>
<thead>
<tr>
<th>Species</th>
<th>Attack direction</th>
<th>5% rammed Attack</th>
<th>Attacking territorial</th>
<th>Abundance of stripe</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>C. eucinostomus</td>
<td>C. pleurotaenia</td>
<td>C. eucinostomus</td>
</tr>
<tr>
<td>C. ortognathus</td>
<td>below, 45°</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. lieni</td>
<td>below, 70-90°</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Undescribed Cichlid</td>
<td>above</td>
<td>-</td>
<td>+</td>
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fish grab each other. In Wilhelm's (1980) laboratory observations, the snout-engulfing was preceded by chasing, ramming and butting. Only when the female was 'exhausted' after these attacks did mouth engulfing take place. We suggest that snout-engulfing reflects laboratory confinements. It is interesting that Wilhelm also reported ramming by the paedophages after which 'some females spat out part of their brood'. Such behaviour is consistent with our observations in Lake Malawi and might be the method these paedophages use to get their food in nature.

Nevertheless, snout-engulfing would increase in importance relative to the usual ramming attack under three conditions: (1) when ramming incapacitated the females enough to allow the paedophages to grab the snout quickly; (2) when low visibility allowed the paedophages to await undetected, facilitating a quick dart and grab before the female could turn or (3) when the cichlids are inactive on the bottom, such as after dark, permitting a frontal approach by the paedophages.

We agree with Wilhelm (1980) that 'paedophagy' should only refer to species feeding off-spring in the mouth of brooding cichlids, but we suggest that the method many cichlids use to obtain these young is to ram or butt a brooding female. This conclusion, based on our field observations, is more consistent with theoretical considerations than are the alternatives that propose that a female voluntarily jettisons her brood or does not flee when confronted by a fish trying to engulf her snout.

Acknowledgments

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REFERENCES


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Fig. 1. *Cynotilapia urhugnahanu* with and without stripe. Photo taken of a single live individual in an aquarium.

Fig. 3. A preserved specimen of the undescribed paedophagous cichlid that attacks females from above.

McKay & Kocher, *Anim. Behav.*, 31, 1
Fig. 2. *Ctenacara hiem* attacking a brooding female *C. eucinostomus*. The top silvery fish is a female with a mouthful of young. The striped fish underneath is *C. hiem*. The fish in the foreground on the nest is a territorial male *C. eucinostomus*.