

## Hunting Strategies of a Lake Malawi Cichlid with Reverse Countershading

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*Tyrannochromis macrostoma* (Regan), a haplochromine cichlid fish endemic to Lake Malawi, Africa, exhibits reverse countershading. It attacks potential prey fishes from an upright, sideways (90° rotation from an upright position), or upside-down (180° rotation from an upright position) positions. Seventy percent of its attacks are from a sideways position. Whenever it was observed attacking from an upside-down position, its prey was stationed below the attacker. When attacking from a sideways position, its prey was below the attacker 25% of the time and on the same plane 75% of the time. When attacking from a normal position, its prey was below the *T. macrostoma* 82% of the time and on the same plane 18% of the time. Data presented herein lend credence to the self-shadow concealment explanation for the selection of countershading. *Tyrannochromis nigriventris* Eccles, a closely related species, does not display reverse countershading but occasionally attacks from an upside-down position.

COUNTERSHADING denotes that one side of an animal's body is darker than the other (Thayer, 1896). Countershading occurs in various vertebrate groups including fishes (Briard, 1978; Konings, 1987), birds (Butcher and Rohwer, 1989), and mammals (Strahan, 1983). In many of these dichromatic organisms, the dorsum is the more darkly pigmented side, which is termed dorsal pigmentary darkening (DPD). Such a pigment pattern may be important in shape concealment via self-shadow concealment (SSC) because, if the dark side of the body is oriented to the light source, shadows on the body are concealed (Kiltie, 1988). Evidence of the benefits of DPD is circumstantial and includes the following: (1) DPD is present in many taxa; (2) the more darkly pigmented sides are usually on the side facing the light source; and (3) DPD camouflages organisms to the human eye (Kiltie, 1988). Ruitter (1956) provided some experimental evidence in support of SSC when he showed that inverted caterpillars were more susceptible to predation by birds than upright caterpillars.

In fishes, pigmentation may be related to certain hunting strategies. For example, in the Lake Tanganyika cichlid, *Lepidolamprologus profundicola* (Poll), there are two distinct color morphs, pale and dark. The dark color form frequently attacks prey from shaded areas, whereas the pale form initiates attacks from open water (Kohda and Hori, 1993). Comparisons of 19 taxa of carnivorous Lake Tanganyika cichlids showed that dichromatic taxa generally chase active prey, whereas monochromatic forms feed on sessile or sluggish prey (Kohda and Hori, 1993). Such evidence supports the hy-

pothesis that DPD serves to increase foraging efficiency in predatory cichlids that hunt active mobile prey.

Alternative explanations to the self-shadow concealment (SSC) hypothesis for DPD exist. Dorsal pigmentary darkening may increase abrasion resistance in nonaquatic species, shield against ultraviolet light, or be important in thermoregulation (Kiltie, 1988). Furthermore, the dorsal surface may be the primary side exposed by prey to predators or by predators to prey; thus the only side for which camouflaging coloration is important (Kiltie, 1988).

Hypotheses that countershading is important in shape concealment and camouflage can be evaluated by examining the behavior and life history of those fishes that exhibit reverse countershading or ventral pigmentary darkening (VPD) to see whether their behaviors are different from those fishes that show DPD. Certain catfishes in the family Mochokidae swim upside-down at night and are characterized by VPD, including *Synodontis nigriventris* David and *Hemisyndontis membranaceus* Geoffroy Saint-Hilaire (Daget, 1948; Poll, 1971; Nagaishi et al., 1989). While swimming upside-down, these species feed on plankton and fine detritus from the water's surface (Bishai and Abu Gideiri, 1963; Holden and Reed, 1972; Lowe-McConnell, 1975). VPD may minimize predation of these fishes, when they are in the upside-down posture (Chapman et al., 1994).

Increased respiratory efficiency also has been linked with swimming upside-down (Holden and Reed, 1972; Roberts, 1975). Chapman et al. (1994) provided evidence that suggested that *S. nigriventris*, which exhibits VPD, expended less

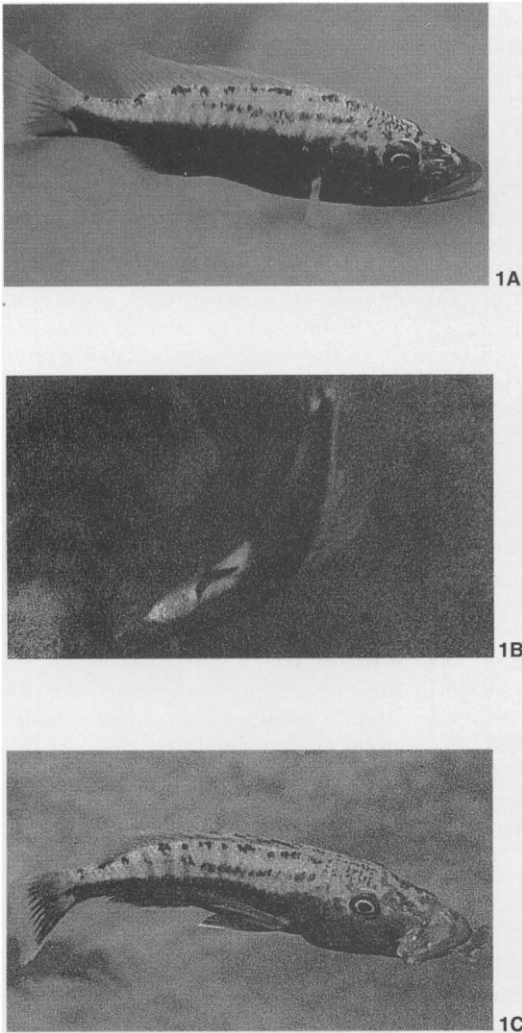


Fig. 1. *Tyrannochromis macrostoma* swimming in a normal position (A), turning 180° (B), and swimming away with a fish in its mouth (C).

energy while swimming upside-down at the water's surface than did *Synodontis afrofisheri* Hilgendorf, which swims in an upright position and does not display VPD. The purpose of this

paper is to describe the hunting behavior of *Tyrannochromis macrostoma* (Regan), a haplochromine cichlid endemic to Lake Malawi that exhibits VPD (Fig. 1).

#### MATERIALS AND METHODS

From 11 March to 1 April, 1985, observations on the feeding behavior of 33 *T. macrostoma* were recorded while SCUBA diving at Mitande Rocks, Cape Maclear, Lake Malawi (14°05'S, 34°54'E). Additionally, we were able to observe the attack sequence of three *Tyrannochromis nigriventer* Eccles, a species that does not exhibit VPD. Fifteen-minute focal samples were conducted; however, some observation periods were interrupted because the fish disappeared into a cave or was lost among the rocks (Table 1). To minimize disturbance, the diver (JRS) watched the fish from 5 m behind and 2 m above. While observing the fish, the following events were recorded: the number of times these two species hovered sideways (90° rotation from an upright position not followed by an attack), the number of times they hovered upside-down (180° rotation from an upright position not followed by an attack), the number of times they attacked from an upright position, the number of times they attacked from a sideways position, the number of times they attacked from an upside-down position, and the total time that each fish was observed. As the fish swam through the water column, it would sometimes pause in an upright position. Because it was not possible to determine whether the fish was observing a potential prey item or just resting, hovers in an upright position were not recorded.

Attacks were defined as a sudden fast movement toward a potential prey. An attack was sometimes initiated from a hovering position, and sometimes it was an extension of a swimming/searching pattern. Because it was difficult to determine whether the attack was successful, success was not recorded.

From January to February 1995, 46 *T. macro-*

TABLE 1. SUMMARY OF THE NUMBER OF ATTACKS AND HOVERS OBSERVED FOR *Tyrannochromis macrostoma* AT MITANDE ROCKS, CAPE MACLEAR, LAKE MALAWI, MALAWI, AFRICA.

Time of day	Number of <i>T. macro.</i>	Tot. min. of obs. per fish	Total attacks upside-down	Total attacks sideways	Total attacks normal	Total hovers upside-down	Total hovers sideways
0800–1200	14	15	19	44	2	18	110
1200–1630	10	15	4	26	0	5	140
0800–1630	4	10–11	0	10	0	1	22
0800–1600	5	3–6	2	8	1	2	15
Totals	33		25	88	3	26	287

TABLE 2. SUMMARY OF ATTACKS RECORDED FROM VIDEO TAPES OF *Tyrannochromis macrostoma* AT MAZINZI REEF, LAKE MALAWI, MALAWI, AFRICA.

Time	No. <i>T. macro.</i>	Total time	Attacks upside-down	Attacks sideways	Attacks normal
0700–1200	28	5:04:33	4	11	10
1201–1600	18	2:19:47	1	5	1
Total	46	7:24:20	5	16	11

*stoma* were individually recorded at Mazinzi Reef (13°53'S, 34°59'E) in Lake Malawi using a Sony 8mm Hi-8 camcorder in an Amphibico underwater housing. By slowing the playback speed and reviewing the tape several times, it was possible to record attack success. The attack frequency, position (i.e., upright, 90° rotation, 180° rotation) of the fish before the attack, the species and the frequency of being attacked, and the total time the individual was recorded on video tape were also enumerated after reviewing the tapes.

#### RESULTS

Both the direct and recorded observations indicated that sometimes *T. macrostoma* would rotate in the water column 180° and attack immediately. In other cases, *T. macrostoma* would swim over the rocks, and small mbuna would hide in the crevices. *Tyrannochromis macrostoma* would rotate 180°, hover in this upside-down position, and wait for the mbuna to emerge from their hiding places, whereupon it would attack.

At Mitande Rocks, 33 *T. macrostoma* were observed for a total of 423 min. Sideways hovering was observed 287 times (40.7 hovers/h) and attacks were often initiated from a sideways position (88; 12.5 attacks/h; Table 1). It hovered upside-down 26 times and attacked upside-down 25 times (3.5 attacks/h). Only three attacks (0.4 attacks/h) were observed from an upright position. Observations of *T. nigriventer* demonstrated that this species also attacks upside-down, even though it does not display VPD.

At Mazinzi Reef, 46 *T. macrostoma* were recorded on video tape for a total of 444 min. During this time, it attacked 16 times from a sideways position (2.2 attacks/h), 11 times from a normal position (1.5 attacks/h), and five times from an upside-down position (0.67 attacks/h). Four of the 16 sideways attacks resulted in prey captures, but none of the attacks from the other positions resulted in captures. Although none of the attacks from the upside-down position resulted in the capture of prey,

while following *T. macrostoma* with a Nikon 35 mm underwater camera, a successful upside-down attack was observed (Fig. 1).

Videos recorded at Mazinzi Reef indicated that *T. macrostoma* would position itself approximately 2–10 cm above the rock substratum. Many of the attacks occurred when *T. macrostoma* swam over a discontinuity with an immediate drop greater than 1 m in the substratum. When *T. macrostoma* attacked from an upright position, the potential prey were on the same horizontal plane 18% of the time and positioned below the attacker 82% of the time. When attacking after turning 90°, the prey were on the same horizontal plane 75% of the time and positioned below the attacker 25% of the time. Every time *T. macrostoma* attacked after rotating 180°, the attack was from above the prey. When potential prey were on the same horizontal plane, *T. macrostoma* would rotate 90° 86% of the time before attacking. When attacking fish from above, *T. macrostoma* would maintain its upright position 50% of time, rotate 90° 22% of the time, and 180° 28% of the time.

Each of the three *T. nigriventer* that were observed for 15-min focal watches attacked sideways three times and hovered in a sideways position for a total of 21 times. Two of the three attacked from a normal position, and one attacked twice from an upside-down position.

#### DISCUSSION

Overall, the *T. macrostoma* observed over Mitande Rocks attacked more frequently than those observed at Mazinzi Reef, perhaps because prey were generally more abundant at Mitande Rocks than at Mazinzi Reef. The majority of observations made at Mitande Rocks was between 2 m and 10 m, whereas those made at Mazinzi Reef were between 10 m and 20 m. As noted by Ribbink et al. (1983), the rock-dwelling fishes are much more abundant at shallower depths.

The observations of *T. macrostoma* rotating 180°, when small mbuna hid in the rock crevices, and attacking when they emerged supports the SSC hypothesis as an explanation for countershading. The observations over Mitande Rocks indicated that *T. macrostoma* initiates the majority of its attacks after its body is rotated 90°. Four of the 16 sideways attacks recorded at Mazinzi Reef resulted in prey being captured. Perhaps *T. macrostoma* was exposing its more cryptic side to the prey, particularly if the background was a boulder or other dark structure. However, this 90° rotation may have simply reduced the predators' profile, thus making it less

conspicuous and was independent of VPD. The second conjecture is supported, because the most often attack posture of *T. nigriventer*, which did not display VPD, was also sideways. Because *T. nigriventer* also on occasion attacked after rotating 180°, there is the question of which came first, form or function.

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