
Notes and records

Ultraviolet radiation enhances zooplanktivory rate in ultraviolet sensitive cichlids

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Introduction

In Lake Malawi, East Africa, a monophyletic lineage of over 700 species of cichlid fish has evolved in the past two million years (Turner *et al.*, 2001). To explain this rapid rate of diversification in Lake Malawi, most researchers invoke theories based on ecological speciation, particularly linked to trophic morphology, and sexual selection (See Danley & Kocher, 2001 for a recent review). Essential to the application of these speciation theories is an understanding of the visual system. Few studies, however, have investigated the visual capabilities of these fish. Recently, R. Jordan *et al.* (unpublished data) found that the presence of ultraviolet (UV) photoreceptors (maximal spectral absorbance between 315–420 nm) varies among species of Lake Malawi cichlids. Given this variability and because UV radiation can cause retinal damage (Tovee, 1995), a functional advantage for maintaining UV sensitivity is expected.

Enhanced ability for zooplanktivory might be one such advantage provided by UV sensitivity (Bowmaker & Kunz, 1987; Loew & McFarland, 1990; Loew *et al.*, 1993; Browman *et al.*, 1994) because UV photoreception can aid visually guided feeding behaviours by two means: (i) increasing contrast between the prey item and the back-

ground (Loew & McFarland, 1990) or (ii) scattering of UV by the prey item, thereby causing a veiling effect (Novales-Flamarique *et al.*, 1992). The rock-dwelling (mbuna) cichlids of Lake Malawi are ideal species with which to study UV sensitivity and foraging because these fish inhabit the shallower depths of Lake Malawi in which substantial presence of UV light is likely (see Loew & McFarland, 1990), and because McKaye & Marsh (1983) observed these fish facultatively feeding on zooplankton. The objective of this study, therefore, was to discern through feeding experiments whether UV sensitivity enhances zooplankton capture in a group of Lake Malawi mbuna.

Methods

We used adults of three UV sensitive *mbuna* species: *Cynotilapia afra*, *Metriaclima benetos*, and *Metriaclima melabanchion*; and three UV insensitive non-rockdwelling species for comparison: *Tyrannochromis macrostoma* (open-water), *Mylochromis lateristriga* (sand-dweller), and *Lethrinops parvidens* (sand-dweller) (Konings, 1995). In our study adults were similar in size [13 ± 0.09 cm in total length (TL)] and were observed feeding on zooplanktonic prey. We classified a species as UV sensitive if we found UV photoreceptor cells in adult retinas and if their corneas and lenses passed ultraviolet light (R. Jordan *et al.* unpublished data). All fish were collected from Monkey Bay in Lake Malawi (14°S–35°E).

We tested twenty-two subgroups of three to six fish drawn from the larger pool of fish (Table 1). Subgroups rather than individual fish were used because some fish fed reluctantly when alone. As we were not concerned with individual species performance, we tested fish in multi-species groups to eliminate dominance behaviours among males. We also varied group sizes to maximize the functional diversity of our feeding groups. Therefore, we focused our statistical analyses on differences among treatments and not among subgroups. In our trials fish were used more than once. To avoid pseudoreplication we ensured that each subgroup was unique in its composition.

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Table 1 Experimental schedule and group composition. Treatment order and number of individuals used

Experiment	UV sensitive (ten fish)		UV insensitive (nine fish)	
	order of treatment	No. of fish	order of treatment	No. of fish
1	UV+,UV-,dim	6	UV+,dim, UV-	5
2	UV-,UV+,dim	6	UV-, dim, UV+	5
3	UV+,UV-,dim	6	UV+,dim, UV-	5
4	UV-,dim,UV+	5	dim, UV-, UV+	4
5	UV+,dim,UV-	5	dim, UV+, UV-	4
6	UV-,dim,UV+	4	dim, UV-, UV+	4
7	UV+,UV-,dim	3	dim, UV+, UV-	4
8	dim,UV-,UV+	3	dim, UV-, UV+	4
9	dim,UV+,UV-	3	UV-, UV+, dim	3
10	dim,UV-,UV+	3	UV+, UV-, dim	3
11	dim,UV+,UV-	3	UV-, UV+, dim	3

Fish were starved for a 24-h period prior to experimentation. Two hours before treatment, two subgroups (one from the UV sensitive group and one from the UV insensitive group) were placed into a single 110-l test tank

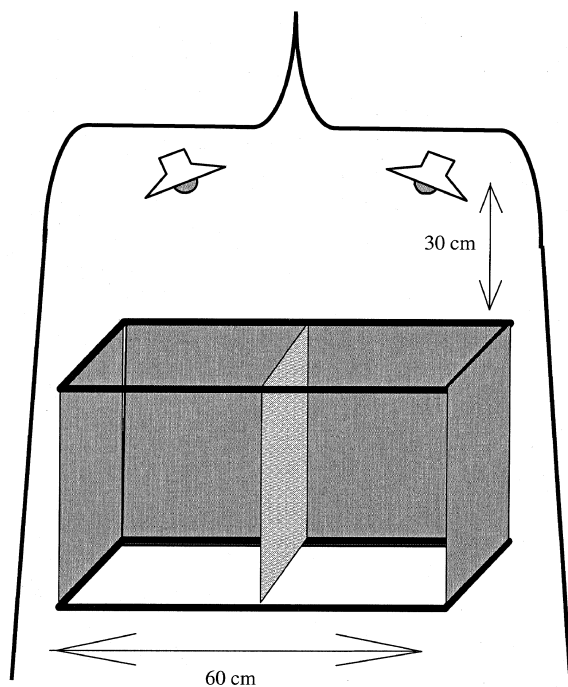


Fig 1 Test tank. The two subgroups were separated by a transparent perforated partition. To ensure that the fish could see the prey in all light treatments we surrounded the tank with poster board that was reflective both in the UV and visible light. Experiments were shielded from ambient light by a light-blocking tent. We used a selenium light meter to inspect for intensity differences among treatments within an experiment (see Hawryshyn, 1982), and then adjusted our lights accordingly

(Fig. 1). During a single experiment, fish were exposed to three treatments equally spaced 20 min apart. These treatments were: UV enriched light (UV+, two 150 W broad-spectrum incandescent bulbs), UV subtracted light (UV-, two 150 W broad-spectrum incandescent bulbs blocked with UV cutoff-filters below 400 nm), and dim (dim, no direct irradiation, but some ambient broad-spectrum). During each of the three treatments, 100 live preys (*Artemia* spp.) were released into one side of the tank by a drop cup with a handle. We previously found that 100 preys were sufficient to allow at least 30 s of feeding while not satiating the fish. After prey administration, we recorded the time for the fish to consume all the prey by viewing through a small hole in the tent and using video for validation. After feeding ceased, the tank was thoroughly inspected for escaped prey, which rarely occurred.

Predation rate was measured as number of prey consumed divided by number of fish in the experiment per unit time (no. prey/no. predators/time). We used paired *t*-tests with Bonferroni corrections (Sokal & Rohlf, 1995) to compare among the three treatments. Paired tests were necessary because of the potential confound with varying group size.

Results

We found that under UV+ radiation, feeding rate was increased in the UV sensitive fish when compared with the UV-treatment (paired *t*-test, $n = 11$ comparisons, $P = 0.021$, t -test = 2.36; Fig. 2). The UV insensitive fish, however, did not exhibit a change in feeding rate (paired *t*-test, $n = 11$ comparisons, $P = 0.173$, t -test = 1.46). Both types fed faster when comparing both light conditions to the dim condition (paired *t*-tests, UV sensitive group:

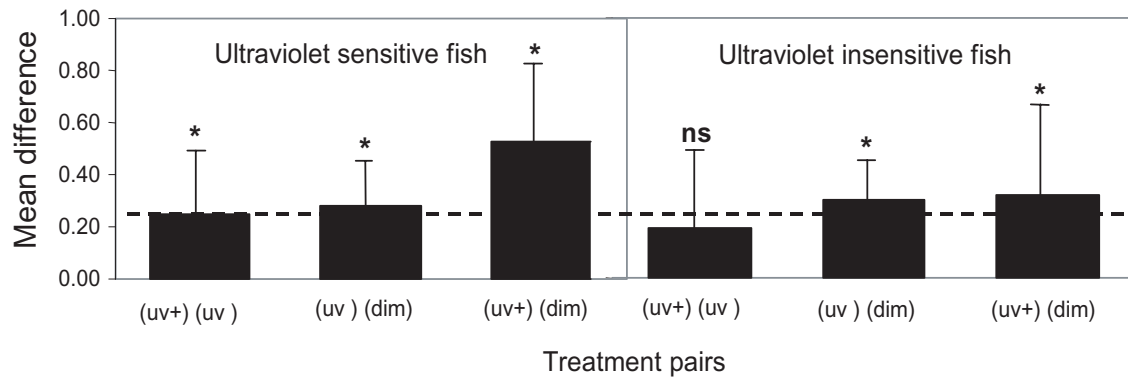


Fig 2 Average paired differences. Average difference with standard deviation error bars taken between treatment pairs for the two experimental groups (i.e. ultraviolet sensitive and ultraviolet insensitive fish). The pairs are listed below each bar. Asterisks indicate that a significant difference was found between those treatment groups (using the paired *t*-test). The broken line is placed at the lowest significant value for visual ease of comparison

$P < 0.001$ for both UV+ and UV-comparisons with dim, $n = 11$ comparisons, t -test = 4.91, 4.38 respectively; and UV insensitive group: $P = 0.002$ for UV+ compared with dim, t -test compared with dim, t -test = 4.39, $n = 11$ comparisons).

Prior to our statistical analysis, we examined our data for the effects of pseudoreplication and treatment order. First, we inspected for potential correlation between individual fish and group feeding rate using Pearson's correlation coefficients. We found no evidence of substantial correlation (UV sensitive: $r = 0.33$, UV insensitive: $r = 0.18$), suggesting independence among groups. Next, we used paired *t*-tests to inspect for the effects of treatment order. We found that treatment order did not have a significant effect within either type of fish tested (UV sensitive group: $P = 0.308$ and UV insensitive group: $P = 0.806$).

Discussion

We found that only the UV sensitive fish increased feeding rate under UV enriched versus UV subtracted or dim conditions. Both UV sensitive and insensitive fish, however, fed at a higher rate in either light condition when compared with the dim condition. These findings not only support the link between enhanced zooplanktivory and UV sensitivity but also emphasize the importance of visual factors in feeding.

Broad generalizations about UV sensitivity are difficult to make, but it seems that while many rock-dwelling (mbuna) fish have UV sensitivity, the more open water fish

may not (R. Jordan *et al.* unpublished data). Given the paucity of field data on feeding habits of Lake Malawi fish, a definitive connection between feeding mode and UV sensitivity cannot be made. Evidence based on feeding apparatus morphology has suggested that the members of the UV sensitive group are not chiefly zooplanktivorous but rather algal scrapers or phytoplanktivores (Fryer & Iles, 1972; Reinthal, 1990). McKaye & Marsh (1983), however, speculate that mbuna are facultative feeders because they observed some algal scrapers switching to zooplanktivory during times of food abundance. Regardless of feeding mode, it is clear that under broad-spectrum lighting UV sensitivity enhanced feeding rate within the UV sensitive group. Thus, it is possible that even if UV sensitivity evolved in response to a selective pressure other than for enhanced zooplanktivory (see Hárosi, 1985; Downing *et al.*, 1986; Garcia & Perera, 2002; Kodric-Brown & Johnson, 2002; Smith *et al.*, 2002 for examples) this sensitivity could still potentially enhance fitness through increased ability for zooplanktivory. It is also clear in both the UV sensitive and insensitive groups, that the visual environment greatly affected feeding ability and likely could affect survival, which highlights the necessity for continued investigation into the visual factors that affect feeding ability.

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