

## Nonvisual feeding in a visual planktivore, *Xenomelaniris venezuelae*

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**Summary.** Studies of the diel feeding patterns of the planktivorous fish, *Xenomelaniris venezuelae*, in Lake Valencia, Venezuela, revealed that, although the fish is primarily a diurnal feeder, it consumes substantial numbers of *Chaoborus* larvae and pupae at night. A number of fish species are known which feed on plankton at night, but these fish are filter feeders and their diets largely consist of relatively small, nonevasive prey. *Chaoborus*, however, is large and agile. Predation by *Xenomelaniris* in the dark was also studied experimentally. Captured fish were placed in completely darkened aquaria with zooplankton from Lake Valencia. After several hours the plankton was removed and examined for evidence of feeding. The fish were found to consume *Chaoborus* pupae and fourth instar larvae but not other types of prey. The mode of feeding by *Xenomelaniris* in the dark is unknown.

that Lake Valencia has dense populations of zooplankton that are exploited by *Xenomelaniris*. Analysis of stomach contents has shown that *Xenomelaniris* feeds to some extent on all zooplankton, including rotifers, cladocerans, copepods, and the dipteran *Chaoborus* (Unger and Lewis 1983). Feeding studies of *Xenomelaniris* and behavioral observations show that the fish captures prey individually. *Xenomelaniris* feeding, like that of other fish that feed by this mechanism, is highly selective. Electivity indices for specific prey types are partly determined by the size of the fish and partly by the size and escape ability of the prey (Unger and Lewis 1983).

After finding zooplankton, especially large *Chaoborus* larvae, in the guts of the fish on the darkest nights, we began to suspect that *Xenomelaniris* is not entirely dependent on vision, although the fish clearly use vision for prey detection when light is available. There is some light near the surface of lakes even on moonless nights. Nevertheless, the ability of *Xenomelaniris* to capture *Chaoborus*, a transparent and agile prey, in nearly total darkness suggested possible nonvisual feeding by a mechanism involving detection of individual prey. We therefore formulated the hypothesis that *Xenomelaniris* is able to detect and capture prey in total darkness. The present paper reports our tests of this hypothesis.

Selective feeding by planktivores often affects zooplankton communities in lakes and ponds (Hall et al. 1976, O'Brien 1979, Zaret 1980). Prey detection, which can be influenced by the size, appearance, or behavior of prey, is a key determinant of prey selection. Invertebrate predators commonly detect their prey by tactile stimuli (e.g., Williamson 1980; Giguere and Dill 1979). In contrast, planktivorous fishes generally either filter water across the gillrakers, thus removing zooplankton from the water by a mechanism that apparently does not involve prey detection (Drenner et al. 1982), or detect their prey visually and capture them individually. For visually feeding fish, much emphasis has been placed on the relationships between illumination, visual acuity, prey visibility, and prey detection (e.g., Vinyard and O'Brien 1976, Confer et al. 1978). It has often been assumed that planktivorous fish that capture prey individually are incapable of detecting prey below some threshold of illumination due to their reliance upon vision. While this is apparently true of some species, our studies of the visual planktivore *Xenomelaniris venezuelae* do not conform to this assumption.

*Xenomelaniris* is a small (maximum size, 9 cm) atherinid that is endemic to Lake Valencia, Venezuela. Lake Valencia is a large eutrophic tropical lake located at 404 m asl in North-Central Venezuela. The lake has been described elsewhere in some detail (Lewis and Weibezahn 1976, Lewis 1983); for present purposes it is only important to note

### Methods

The *Xenomelaniris* population was sampled weekly between April 1979 and October 1980. Night samples were taken approximately every other week for most of this period. In all instances, the fish were captured with a large hoopnet. Stomach content analysis was done by methods described in Unger and Lewis (1983).

The nonvisual feeding capabilities of *Xenomelaniris* were tested experimentally in a field laboratory near Lake Valencia. There were 3 separate experiments, all of which were conducted in October of 1980. A few days prior to each experiment, fish ranging in length from 47 to 55 mm were taken from Lake Valencia and transported to the laboratory, where they were placed in an aquarium and allowed to acclimate to laboratory conditions. The fish were fed daily with plankton from Lake Valencia. The aquaria used in the experiments were kept in a room that could be completely darkened. As extra insurance against small amounts of illumination, the experiments were carried out at night and each aquarium was wrapped with sheets of black plastic.

For experiment 1, 14 fish were allowed to acclimate for 1 week in a 40-l aquarium. On the night of the experiment, a plankton sample that included *Chaoborus* larvae and pupae was taken from Lake Valencia with a net and brought to the lab in a large tank. The tank was agitated vigorously and plankton aliquots were removed for addition to a dark aquarium with fish (treatment), and to a second identical aquarium without fish (control). Additional aliquots were taken from the tank and preserved. The preserved aliquots were subsequently counted to provide estimates of the initial zooplankton abundances and the variance among aliquots. In the early morning hours, the fish were removed and the zooplankton of both the control and the experimental aquaria were filtered through a plankton net and preserved. Total counts were made for *Chaoborus*. Other categories of prey were too abundant to be counted by this method and were therefore subsampled.

In experiment 2, the conditions of experiment 1 were reproduced except that plankton without *Chaoborus* was used. *Chaoborus* is a nonvisual planktivore and is a preferred food of *Xenomelaniris*. The absence of *Chaoborus* in experiment 2, therefore, served two purposes: 1) to assess the impact of *Chaoborus* predation on zooplankton abundances in experiment 1 and 2) to provide as much inducement as possible for fish to feed in the dark on items other than *Chaoborus*.

In the third and final experiment, a single acclimated specimen of *Xenomelaniris* was confined in a dark aquarium for 2 h with 40 *Chaoborus* of instar 4. At the end of the experiment, the remaining larvae were removed and counted. The density of fish and prey per unit volume of water were comparable to those in the lake in this experiment, whereas in experiments 1 and 2 the densities of both fish and prey were higher than in the lake.

Replicate aquaria for treatment and control were not used in any of the experiments because facilities at our field lab were limited and because *Xenomelaniris* is difficult to culture. For this reason we used for experiments 1 and 2 a one-tailed t-test for comparing a single observation with a sample mean (Sokal and Rohlf 1981) to test for differences between initial prey abundances and final abundances in the aquaria. No statistical test was made of the results of the third experiment because sampling error was zero (complete counts).

## Results

Table 1 summarizes the nocturnal feeding of *Xenomelaniris* in Lake Valencia. The samples included in the table were all taken between midnight and first light (0500). Because the stomach clearance time in *Xenomelaniris* is about 45 min (Unger, unpublished), any food items in the stomach at this time of night would have to have been consumed after sundown.

Table 1 shows that *Chaoborus*, a favored food of *Xenomelaniris* that is consumed in large quantities during daylight hours, is also captured by the fish at night. The table also shows that other food items are taken at night, but the total biomass represented by them is much less than for *Chaoborus*. Feeding occurs whether or not there is moonlight. There is considerable variation in the amount of feeding on different dates, and this is partly explained by a seasonal trend in the availability of *Chaoborus* in the feeding zone (Saunders 1980). Differences between the

**Table 1.** Summary of *Xenomelaniris* stomach contents for fish collected between 0100 and 0500

	Prey in fish stomachs, dry mass ( $\mu\text{g}$ ) per fish				Number of fish
	<i>Chaoborus</i> Pupae	<i>Chaoborus</i> In. 4	<i>Chaoborus</i> In. 1, 2, 3	Other Zoo- plank- ton	
Moonlit Nights					
15 September 1979 <sup>a</sup>	18	1460	44	0	11
8 December 1979	0	2711	55	8	16
4 April 1980	0	0	0	1	10
5 April 1980	0	71	0	11	10
30 May 1980	0	13	0	6	11
28 June 1980	0	0	0	0	8
23 August 1980	10	57	0	1	20
28 August 1980	36	297	11	6	50
No Moon					
4 April 1979	0	0	0	1	10
15 September 1979 <sup>a</sup>	8	939	53	1	25
20 April 1980	0	0	0	3	12
4 October 1980	38	200	3	1	16
19 October 1980	22	95	0	0	9

<sup>a</sup> On 15 September 1979 fish were sampled at 0230 and at 0500. Since moonrise on this night was at 0322, entries for this date are made both under the 'Moonlit Nights' and under the 'No Moon' headings

moonlit nights and moonless nights in the consumption of *Chaoborus* was tested by analysis of covariance, with *Chaoborus* availability as a covariate. No statistically significant difference exists ( $P > 0.05$ ).

Figure 1 summarizes the 24-h feeding pattern of 3 major size classes of *Xenomelaniris* in Lake Valencia. The Fig. shows the average stomach content at several times of day over nearly two years of study. Although the Fig. shows the amount of prey present in the stomach, clearance time is sufficiently short (45 min) that conclusions about time of ingestion can be made from the figure. Feeding is unquestionably more intense during daylight hours, especially near dawn, than it is at night. Nevertheless, substantial feeding does occur at night, contributing close to 30% of the daily ration for fish of all sizes. The Fig. indicates that nocturnal feeding is almost entirely restricted to *Chaoborus*. The mean rate of nocturnal consumption of *Chaoborus* by mid-sized fish is about 0.5 mg (dry weight) fish<sup>-1</sup> h<sup>-1</sup>.

Table 2 summarizes the results of the 3 experiments. In the first experiment, there were significant differences in abundances between initial and treatment (containing fish), and between initial and control (containing no fish) aquaria for half of the prey categories. All reductions of prey other than fourth larval instars and pupae of *Chaoborus* were about the same in the control and treatment tanks, indicating that fish feeding had no significant effect on abundances of these prey. These reductions are probably attributable to *Chaoborus* predation. The reductions of *Chaoborus* larval instars 2 and 3 in the control aquarium suggest cannibalism by instar 4 larvae, an unexpected but not unprecedented finding (Parma 1971). Abundances of *Chaoborus* instar 4 and pupae were significantly reduced in the treatment tank but not in the control tank. This demonstrates that the fish were able to capture these large prey in the dark.

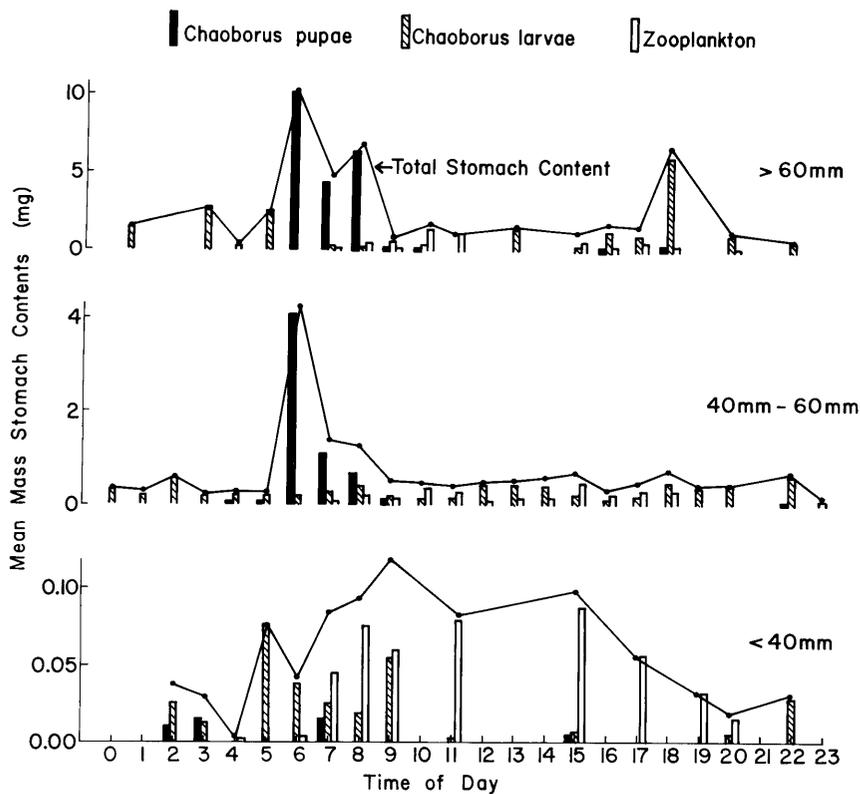


Fig. 1. Average mass of food in the gut of 3 major size classes of *Xenomelaniris* at all times of the day

Table 2. Summary of results of experiments 1-3. Initial abundances compared with control and treatment abundances using one-tailed t-test for comparison of a single observation with a sample mean (Sokal and Rohlf 1981)

Prey type	Experiment 1				Experiment 2				Experiment 3			
	Initial		n	No Fish	With Fish	Initial		n	No Fish	With Fish	Initial	Final
	$\bar{x}$	SD				$\bar{x}$	SD					
<i>Chaoborus</i>												
pupae	199	5	3	211	112**	-	-	-	-	-	-	
instar IV	1,377	71	3	1,242	969*	-	-	-	-	40	28	
instar III	765	26	3	528**	449**	-	-	-	-	-	-	
instar II	66	6	3	29*	18*	-	-	-	-	-	-	
Copepods												
<i>Notodiaptomus venezolanus</i>												
adult females	1,354	505	24	1,244	1,502	-	-	-	-	-	-	
adult males	1,729	834	24	1,931	2,711	-	-	-	-	-	-	
<i>Mesocyclops decipiens</i>												
adult females	12,312	1,700	24	8,844*	9,268*	1,217	642	21	1,148	1,102	-	
adult males	12,150	1,679	24	8,575*	9,194*	8,354	1,164	21	9,200	8,759	-	
juveniles copepodids	28,750	3,096	6	14,857**	17,143**	-	-	-	-	-	-	
Cladocerans												
<i>Moina micrura</i>	-	-	-	-	-	16,543	1,659	21	13,562*	14,335	-	
<i>Ceriodaphnia cornuta</i>	75,833	6,303	6	52,525**	51,394**	11,915	3,334	21	10,688	9,616	-	
Rotifers												
<i>Brachionus calycifloris</i>	-	-	-	-	-	12,936	1,883	21	10,438	12,755	-	
Other rotifers	1,167	619	6	500	586	4,438	1,143	21	3,500	3,541	-	

\*  $P < 0.05$  \*\*  $P < 0.01$

In experiment 2, which excluded *Chaoborus* so as to isolate its effects both as planktivore and as prey, no significant reductions of prey abundances occurred except for *Moina*, a cladoceran, in the control tank. Abundances of most prey categories appear to have been slightly reduced

in both treatment and control aquaria. Since the prey used in this experiment are all small-bodied species, this reduction is probably due to the loss of some individuals in transferring the plankton from the aquaria to sample bottles. If this loss in transfer had been deducted from the observed

reduction for *Moina* in the control aquarium, it is unlikely that any reduction remaining would have been significant. The results of this experiment support our contention that the reductions of prey categories other than *Chaoborus* in experiment 1 are largely due to *Chaoborus* predation. Furthermore, since abundances of prey were about the same in the treatment and control aquaria at the end of experiment 2, there is no evidence of significant fish feeding on these prey types. Exclusion of *Chaoborus* as a prey item did not induce feeding by the fish on other prey in the dark.

In experiment 3 there was a substantial reduction of the *Chaoborus* instar 4 larvae in the presence of a single fish. The rate of consumption of *Chaoborus* in the experiment was 0.6 mg (dry weight) fish<sup>-1</sup> hr<sup>-1</sup>. The estimated rate of consumption of *Chaoborus* in experiment 1 was 0.4 mg (dry weight) fish<sup>-1</sup> hr<sup>-1</sup>. These rates are comparable to the rate of nocturnal feeding on *Chaoborus* by *Xenomelaniris* as estimated from the field data.

### Discussion

The field data show that considerable *Xenomelaniris* feeding occurs at night, even in the absence of moonlight, and that this feeding is highly selective for larger sizes of *Chaoborus*. The laboratory experiments show that *Xenomelaniris* in fact requires no light whatever to feed on large sizes of *Chaoborus*, but that its ability to feed on other kinds of food is reduced to a negligible level by complete darkness. In view of the transparency of *Chaoborus* larvae and the rapid extinction of light in Lake Valencia (secchi depth, 1.5–2.5 m) nonvisual capture of *Chaoborus* by *Xenomelaniris* may play a role in diurnal feeding as well.

The ability of *Xenomelaniris* to capture *Chaoborus* in the dark is somewhat surprising because these prey are highly mobile and are able to detect water movement (Giguere and Dill 1979). Drenner and McComas (1980) found that *Menidia beryllina*, an atherinid fish which is similar in many respects to *Xenomelaniris*, can also feed in the dark. This fish, however, consumed mostly small, non-evasive prey, as consistent with a filtering mode of feeding. *Xenomelaniris* capture of *Chaoborus* in the dark is clearly by some mode other than filter-feeding because *Chaoborus* are highly evasive prey (Drenner et al. 1978). Townsend and Risebrow (1982) demonstrated that the common bream, *Abramis brama*, can detect and capture *Daphnia* at light intensities approaching 0 lux. The authors suggest that the fish locate *Daphnia* by sensing hydrodynamic disturbances of the swimming *Daphnia*. *Chaoborus* is much larger than the other prey of *Xenomelaniris* (Unger and Lewis 1983) and undoubtedly disturbs the water more when it swims. The lateral line system of many fish is highly sensitive to water movements (Dijkgraaf 1962) and may be involved in the capture of *Chaoborus* by *Xenomelaniris* in the dark. Hoekstra and Janssen (personal communication) have shown that blinded mottled sculpin, *Cottus bairdi*, detect and capture prey by means of this sensory system.

Our results demonstrate that *Xenomelaniris* can detect and capture prey in total darkness. This adaptation may greatly enhance the ability of the *Xenomelaniris* population

to exploit its food resources in Lake Valencia. Nonvisual detection of prey may play an important role in the feeding of other planktivorous fish as well.

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### References

- Confer JL, Howick GL, Corzette MH, Kramer SL, Fitzgibbon S, Landsberg R (1978) Visual predation by planktivores. *Oikos* 31:27–37
- Dijkgraaf S (1962) The functioning and significance of the lateral line organs. *Biol Rev* 38:51–105
- Drenner RW, DeNoyelles Jr F, Kettle D (1982) Selective impact of filter-feeding gizzard shad on zooplankton community structure. *Limnol Oceanogr* 27:965–968
- Drenner RW, McComas SR (1980) The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In: Keerfoot WC (ed) *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, pp 587–593
- Drenner RW, Strickler RJ, O'Brien WJ (1978) Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *J Fish Res Board Can* 35:1370–1373
- Giguere LA, Dill LM (1979) The predatory response of *Chaoborus* larvae to acoustic stimuli, and the acoustic characteristics of their prey. *Z Tierpsychol* 50:113–123
- Hall DJ, Threlkeld ST, Burns CW, Crowley PH (1976) The size efficiency hypothesis and the size structure of zooplankton communities. *Ann Rev Ecol Syst* 7:177–208
- Lewis WM Jr (1983) Temperature, heat and mixing in Lake Valencia, Venezuela. *Limnol Oceanogr* 28:273–286
- Lewis WM Jr, Weibezahn FH (1976) Chemistry, energy flow, and community structure in some Venezuelan fresh waters. *Arch Hydrobiol Suppl* 50:145–207
- O'Brien WJ (1979) The predator-prey interaction of planktivorous fish and zooplankton. *Am Sci* 67:572–981
- Parma S (1971) *Chaoborus flavicans* (Meigen) (Diptera, Chaoboridae): an autoecological study. Dissertation. University of Gronigen, Rotterdam, Netherlands
- Saunders JF III (1980) The role of predation as a mechanism for controlling planktonic herbivore production in Lake Valencia, Venezuela. Dissertation. University of Colorado, Boulder, Colorado, USA
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd ed, WH Freeman, San Francisco
- Townsend CR, Risebrow AJ (1982) The influence of light level on the functional response of a zooplanktonivorous fish. *Oecologia* (Berlin) 53:293–295
- Unger PA, Lewis Jr WM (1983) Selective predation with respect to body size in a population of the fish, *Xenomelaniris venezuelae* (Atherinidae). *Ecology* 64:1136–1144
- Vinyard GL, O'Brien WJ (1976) Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J Fish Res Board Can* 33:2845–2849
- Williamson C (1980) The predatory behavior of *Mesocyclops edax*: predator preferences, prey defenses, and starvation induced changes. *Limnol Oceanogr* 25:903–909
- Zaret TM (1980) *Predation and Freshwater Communities*. Yale University Press, New Haven

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