

## Why do electric fishes swim backwards? An hypothesis based on gymnotiform foraging behavior interpreted through sensory constraints

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Received 27.11.1991 Accepted 1.4.1992

**Key words:** Electrosensation, Locomotion, Gymnotiform swimming mode, *Apteronotus albifrons*

### Synopsis

Fishes producing high-frequency wavelike electrical discharges maintain a relatively rigid body axis and swim forwards and backwards with equal ease. Using stop-action videotape filming we have observed the gymnotiform *Apteronotus albifrons* feeding on zooplankton and oligochaete annelids. Here it is reported that reverse swimming is characteristic of two foraging behaviors: searching for prey and assessing it. In assessing a potential prey item, fish typically scan it from tail to head by swimming backwards, then ingest it after a short forward lunge. A scan in the opposite direction – from head to tail by forward swimming – would have the prey located near the tail and out of position for the final lunge. Food choice experiments indicate that these electrosensing fish feed equally well, and take larger rather than smaller zooplankton, under light and dark conditions. Furthermore, electric fish take normal (light) colored and darkened prey (*Daphnia*) in a 50:50 ratio under both dark and light conditions. These results are consistent with the interpretation that electrosensory cues are being used to detect zooplankton and other prey. Together, our observations support Lissmann's (1958, 1974) and Lissmann & Machin's (1958) assertion that backwards swimming is a component of a locomotory pattern guided by the constraints produced by an active electrical sense.

### Introduction

Weakly electric teleosts that produce high-frequency electrical discharges swim backwards with the same proficiency that they and other fishes swim forwards. This method of swimming has been termed the gymnotiform mode by Breder (1926) and is characterized by anal fin undulation. (In these fish the dorsal and pelvic fins are absent, the caudal fin is vestigial; see Fig. 1.) Blake (1983) studied the kinematics of this swimming mode and concluded that these are specialized for slow, highly maneuverable locomotion. Further, Blake

(1983) interprets this type of swimming as having 'evolved primarily as an efficient means of foraging in a "complex" environment'.

In contrast, Lissmann (1958, summarized in Lissmann 1974) has grouped gymnotiform swimming with the swimming of *Gymnarchus niloticus* (an African electric fish that swims by undulating its elongate dorsal fin; its anal, pelvic, and caudal fins are absent), and of the marine skates in the family Rajidae, which undulate the tips of their expanded pectoral fins. In particular, Lissmann (1958, 1974) emphasized the relationships between these similar swimming modes and the shared, but homoplastic

(Bullock et al. 1983, Finger et al. 1986) presence of an electric sense. Lissmann states: '*Gymnarchus*, the gymnotids [sic] and skates all share one obvious feature: they swim in an unusual way. *Gymnarchus* swims with the aid of a fin on its back; the gymnotids have a similar fin on their underside; skates swim with pectoral fins stuck out sideways like wings. They all keep the spine rigid as they move. Since few fishes swim in this way or have electric organs, and since the fishes that combine these features are not related, a mere coincidence is unlikely' (1974, p. 61).

The differences between the interpretations of Blake and Lissmann are not trivial. In Lissmann's view, Breder's gymnotiform appearance and swimming mode are clear morphological and behavioral indicators of the presence of an electrosense. In Blake's view, any fish living in an environment requiring high maneuverability might evolve the gymnotiform swimming behavior.

Our purpose is to describe the foraging behaviors of gymnotiform fishes in light of these two interpretations and to resolve this controversy. In particular we determine, with the assistance of stop-action videotape filming, the feeding behavior of *Apteronotus albifrons* foraging on natural prey (zooplankton crustaceans and oligochaete annelids). Further, we run a series of food choice experiments to examine the foraging characteristics of these electrosensing fish. A portion of these results has appeared in abstract form (Lannoo & Lannoo 1990).

## Materials and methods

All observations and experiments were conducted at the Iowa Lakeside Laboratory in northwestern Iowa. After our initial species designation, generic names will be used to identify animals.

### Animals

Adult *Apteronotus* (*Sternarchus*) *albifrons* were purchased from a commercial supplier. Fish ranged from 95 to 120 mm total length. Electric organ dis-

charge (EOD) rates (which within a species vary with fish size and sex, and water temperature) varied between 750 and 820 Hz, corresponding to reported frequencies for this species (e.g. Erskine et al. 1966, Hopkins 1976, Hoshimiya et al. 1980). Fish were maintained individually in 6l, all-glass aquaria and fed predominantly zooplankton, but occasionally other aquatic invertebrates were used for two weeks prior to the start of our tests. The prey used, *Daphnia pulex*, were netted from Miller's Bay in West Lake Okoboji. *Daphnia* used in our feeding experiments were sized by hand using eyedroppers. Large *Daphnia* were defined as over 1.5 mm carapace length, small *Daphnia* were less than 1.0 mm. To darken the carapace and intestine of *Daphnia*, they were held for at least 12 h prior to each trial in water to which several drops of carbon particles (India ink) had been added. Only the darkest *Daphnia* were collected and used. Our preliminary trials confirmed the observations of Lissmann (1958) that EOD discharges have no observable effect on the behavior of *Daphnia* and other invertebrate prey.

Fish could not be obtained in large numbers; during our feeding trials eight individuals were used. To partially compensate for these small numbers, each fish was tested between seven and 14 times for each treatment, although statistics were calculated using individual fish, not trials, as our experimental unit (see Results). The total number of trials for each treatment ranged from 68-77.

### Observations

Gymnotiforms are reported to feed on numerous types of small and large invertebrates in nature (Ellis 1913, Knoppell 1970, Mago-Leccia & Zaret 1978, Hagedorn 1986). Therefore, we observed *Apteronotus* feeding on a wide variety of invertebrates including zooplankton, larger crustacean species, oligochaete annelids, and insect larvae and naiads, in containers of different shapes and sizes. Fish in shallow square and round containers were videotaped while feeding on *Daphnia* and oligochaete annelids (*Lumbriculus variegatus*). Fish were filmed at 30 frames sec<sup>-1</sup> for a total of 90 min using

a Panasonic Omnimovie VHS HQ videorecorder equipped with a macro lens and a high speed (1/500 sec exposure) shutter. Some photographs of feeding fish were taken directly from stopped videotape frames shown on a television monitor. Other photographs of feeding fish were taken with a Nikon 35 mm SLR camera using black and white film (ASA 100).

### Experiments

Experiments with fish were run in all glass, shallow, circular containers, 192 mm in diameter, filled to a depth of 40 mm with 1.2 l of filtered lake water. Water temperatures reflected ambient temperatures and therefore fluctuated, ranging between 18 and 27° C. Fish were divided into two groups and light and dark conditions were run simultaneously (see below). This allowed temperatures to be equivalent between treatments, both for any given set of trials and between trials overall.

Water conductivity, which affects the range of a fish's electric field, was approximately  $400 \mu\text{Siemens cm}^{-1}$  and varied slightly between days but not consistently up or down over the course of our experiments.

The light condition was an open bench top lit by indirect sunlight, augmented by 40 watt fluorescent lights located 2 m above the tanks. The dark condition (these fish are typically nocturnal; Steinbach 1970) was the inside of one of two unplugged refrigerators (0.45 m<sup>3</sup> capacity). The refrigerators were located in the same room where the light condition treatments were run and were at the same ambient temperature as the room. With the door closed, the inside of each refrigerator was completely dark. Animals kept inside exhibited an overall lightening of their epidermis due to melanophore shrinkage, a characteristic response to dark conditions.

Fish were placed singly into their experimental tanks. Tanks were then divided into two groups and put in either ambient light or dark conditions. Fish were allowed to acclimate for between 20 and 30 min, then either 10 large and 10 small, or 10 naturally-colored and 10 darkened *Daphnia* were placed into each tank, where fish fed on them.

Under light conditions we watched fish feed from a distance (gymnotiforms do not appear to be disturbed by silent observers, perhaps because they do not use visual cues, Lissmann 1974, see also Discussion) and allowed individual fish to feed until about 1/2 to 3/4 of their prey had been ingested. Fish clearly fed faster with experience: initial trial times lasted 1 h, but by the third week times were reduced to between 5 and 10 min. Part of this increase in feeding rate may have been due to having more experience with the prey, but perhaps also to a familiarity with the disturbance caused by handling between experimental trials.

Under dark conditions, the time it took fish to take 1/2 of the prey offered, and therefore the length of the trial, was estimated from fish in light conditions and our familiarity with the feeding rates of individual fish. Because we were most interested in the sensory mechanisms these fish use to locate prey, as reflected in their patterns of prey choice, we focused on the ratio of prey classes taken, not overall feedings rates. At the end of each trial, surviving *Daphnia* were removed, sorted by class (size or color), and counted.

### Statistics

For the statistical analysis, each fish was treated separately, as an experimental unit, and the numbers of surviving *Daphnia* obtained for all trials in each treatment were summed. Therefore, for comparisons between treatments, eight numbers – each representing a fish – were used. Preference for individual prey classes was determined by calculating Manly's alpha values for variable prey populations (Manly et al. 1972) for each prey class in each treatment. This test determines deviation from a random sampling of prey when the numbers of individual prey are changing. Because we did not replace ingested prey over the course of a trial, this is an appropriate test (Krebs 1989). After calculating the alpha (relative preference) values, numbers were ranked and tested for significant differences using Mann-Whitney U tests. We tested for size or color preferences both within and between the light and dark conditions.

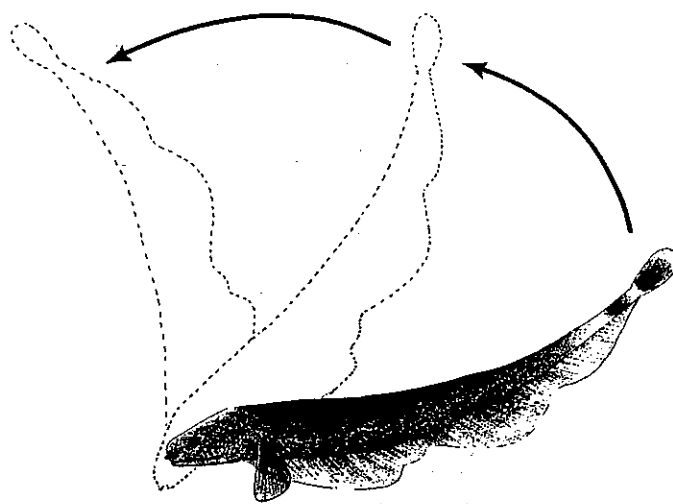


Fig. 1. A representation of the 'side-searching' behavior exhibited by *Apteronotus albifrons* when foraging in shallow, circular containers as seen from above. Fish turn on their side and circle within the tank, with their dorsum leading. Neither side of the fish seems to be preferred, and therefore fish may circle either clockwise or counterclockwise. This behavior is not seen in non-foraging fish. Prey are most often detected along the trunk and tail, reinforcing the idea that vision is not being used to detect these prey. This fish was 105 mm total length.

## Results

*Apteronotus albifrons* actively search for prey by constantly moving throughout their aquarium. Locomotion occurs in both forward and reverse directions and depends on a series of complicated anal and pectoral fin movements in combination with shallow body bends, as the fish propel and position themselves. The pattern of searching is variable and modified to the shape and depth of water in their tank. In its simplest form, searching consists of swimming in a normal horizontal orientation in forward and reverse directions. Fish swam in reverse more often than they swam forwards.

A second, more complicated mode of searching may have been specialized to the feeding behavior in our experimental tanks. In these shallow (2 1/2 fish body depths deep), circular tanks, fish searched for prey by circling. During this behavior, which is probably natural (all fish commonly exhibited it, but only when they were feeding) although specialized, fish positioned themselves with their heads near the center of the tank and their tails directed outward, then rotated 90° around their long axis so that one flank was facing the tank bottom. In this position fish swam in a circular

fashion with their dorsal surface leading – like the hand of a clock – around the inside of the tank (Fig. 1). We term this behavior 'side searching'. Fish placed in these tanks in the absence of prey did not exhibit this behavior. We timed seven side searches, filmed on videotape, of a 105 mm fish through either 90°, 180°, or 360° arcs and found circling speeds of between 60° and 144° sec<sup>-1</sup>.

### *Prey detection, evaluation, reverse approach*

During the search, prey were usually detected near the fish's trunk or tail. At this point the fish would stop searching (i.e. stop, alternate forward and reverse swimming, or side searching) and would immediately approach and scan the prey, usually by reverse swimming. During the scan, fish tended to arch their body laterally with their concave side facing the prey, and swam close to the prey with their tail, trunk, and head following the same arc. Reverse swimming speeds were variable but for seven fish ranged between 10.5 and 15.5 cm sec<sup>-1</sup> (about 1 to 1.5 body lengths sec<sup>-1</sup>; Fig. 2a). Fish stopped reverse swimming when the prey was located in front of them, which put the fish in a

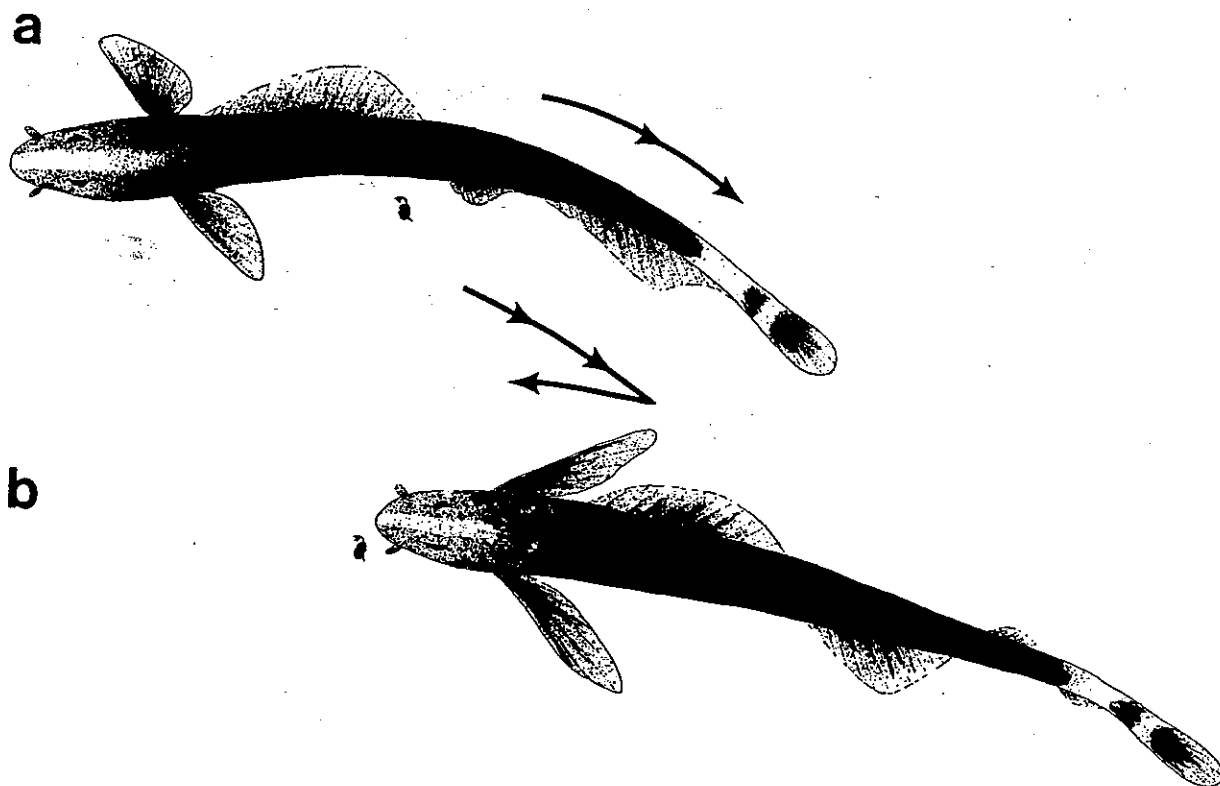


Fig. 2. An *Apteronotus albifrons* depicted scanning a zooplankter, representing *Daphnia pulex*, by reverse swimming. Arrows above the fish show the direction of locomotion. These drawings represent: a – scanning prey by backwards swimming. b – the final lunge, where the fish thrusts forwards at a prey in front of its snout. The fish used for these drawings was 105 mm total length.

position to make its final lunge. To stop, the fish ceased undulating its anal fin and abducted and held its pectoral fins vertically.

#### *Forward approach, prey ingestion*

After being scanned by the fish, the prey was usually positioned in front of, or to the side of, the fish's mouth. Fish then lunged forward to engulf and capture it (Fig. 2b). During the forward lunge, the anal and pectoral fins were used for propulsion. Near the end of the lunge the paired pectoral fins were splayed to stop the fish's forward momentum and the mouth was opened. Zooplankters were ingested by using shallow suction. At the time of ingestion the hyoid apparatus was depressed (Fig. 3); this movement is consistent with generating the negative buccal pressure necessary for ingesting prey with suction (Lauder 1985).

#### *Feeding preferences*

##### *Prey size*

In our feeding experiments *Apteronotus* took more large than small *Daphnia* under both light and dark conditions by about a 2 : 1 ratio; this difference was statistically significant (Table 1a). Under light conditions we observed *Apteronotus* frequently passing over smaller prey to take larger ones. There was no difference in prey size preference between light and dark results. Although we did not quantify feeding rates, we stopped the light and dark trials at the same time, and feeding rates were about equal between light and dark treatments (over the course of our experiments a total of 1775 *Daphnia* were taken under light conditions, 1878 under dark conditions).

##### *Color preference*

*Apteronotus* took darkened and naturally colored

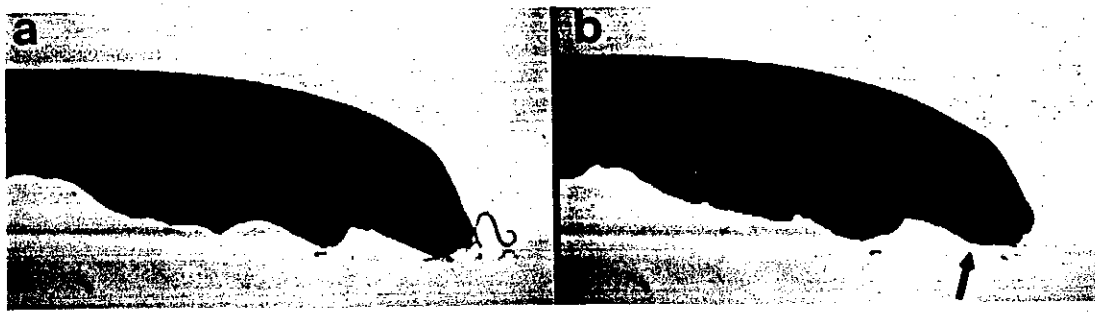


Fig. 3. Photographs taken 30 msec apart of an *Aptereronotus albifrons* using suction feeding to ingest the oligochaete *Lumbriculus variegatus*. Photographs were taken directly from a videomonitor, using freeze frame to stop the tape. a – the final stages of the lunge. b – ingestion: note the ventral bulge caused by the depression of the hyoid apparatus (arrow). This fish was 100 mm total length.

prey in a 50 : 50 ratio under both ambient light and dark conditions (Table 1b).

## Discussion

### Foraging mode

The two characteristics of the foraging behavior of *Aptereronotus albifrons* are: (1) an active searching for individual prey; and (2) a strong tendency to approach and scan an individual prey by backing up over or alongside it. These behaviors differ from those exhibited by visually-mediated zooplanktivores, such as the bluegill sunfish *Lepomis macrochirus*, and the tiger salamander *Ambystoma tigrinum*, which search for prey from a stationary position, detect prey in front of them, and approach

prey head on (Brooks & Dodson 1965, Werner & Hall 1974, Vinyard & O'Brien 1976, Zaret 1979, Janssen 1982, Lannoo 1986, Ehlinger & Wilson 1988). The foraging behavior of *Aptereronotus* – particularly backwards swimming – is consistent with the interpretation that they are not using visual cues and instead may be using electrosensory cues to detect prey (Lissmann 1958, 1974). As Bullock & Szabo (1986) have pointed out however, this is much more difficult to determine than might be expected. For example, *Aptereronotus* produces a wave-like electric organ discharge, which does not vary in frequency as prey are detected and ingested, and therefore changes in electrical discharges cannot be used as a behavioral indicator of electro-detection.

Table 1. a – A comparison of Manly's alpha values (relative preference values; Manly et al. 1972) for *Aptereronotus albifrons* feeding on large (>1.5 mm) and small (<1.0 mm) *Daphnia pulex* under ambient light and dark conditions. Results show that large prey were preferred independently of the light regime. b – Alpha values for *Aptereronotus* feeding on similarly-sized blackened and naturally colored *Daphnia* under light and dark conditions. Results show that prey were not taken on the basis of their visibility in either light regime.

	Mean alpha values		Probability
	large (range)	small (range)	
a Prey size:			
Conditions:			
light	0.67 (0.50–0.74)	0.33 (0.26–0.50)	< 0.01
dark	0.70 (0.52–0.79)	0.30 (0.21–0.48)	< 0.01
b Prey color:	blackened (range)	natural (range)	
Conditions:			
light	0.55 (0.40–0.76)	0.45 (0.24–0.60)	> 0.05
dark	0.52 (0.46–0.56)	0.48 (0.54–0.44)	> 0.05

### Searching

*Apteronotus* search for prey actively by backward and forward swimming – constantly reversing directions. In shallow round containers with a radius of about one body length, these fish search for prey by rotating onto their side and circling through the water at a speed of 1–1 1/2 body lengths  $\text{sec}^{-1}$ . Both sides of the animal are used; neither side seems to be preferred. Side searching was exhibited by all eight of the *Apteronotus* observed, but was restricted to when they were feeding in the shallow circular containers. In nature, side searching may be used in similar shallow, restricted areas.

### Scanning and lunging

*Apteronotus* typically detect prey near their body or tail and then scan it, perhaps to receive an electrical image that they then use to evaluate the prey. Heiligenberg (1975) noted that electroreception systems lack an image focusing mechanism, such as an optical lens, and that electrical images are thus 'blurred'. The function of scanning prey may be to pass an object across a large number of spatially separated electroreceptors in order to compensate for this limitation in image quality. We have frequently observed *Apteronotus* passing over smaller prey to take larger ones. Two possibilities arise: either *Apteronotus* are not detecting the smaller prey, or they are detecting both the larger and the smaller prey and choosing the larger prey.

Electrophysiological and behavioral studies have indicated that electric fish can only detect objects in their near field (Belbenoit 1970, Heiligenberg 1973, 1975, Bastian 1975a,b 1981a,b). Lissmann (1951, 1958) provides the first discussion of this possibility in stating that swimming backwards while avoiding obstacles, finding a way through crevices in rocks, and locating prey 'makes it extremely unlikely that either the poorly developed eyes, or any conventional concepts of perception of water currents or water pressure through the lateral line, could account for such a performance'. In our interpretation, scanning prey for the purpose of foraging is highly dependent on backwards swimming. Scanning by forward swimming puts the prey near the tail and out of position for a

short, accurate lunge. The final lunge is short and accomplished by forwards swimming.

### Function and evolution of the gymnotiform swimming mode

Lissmann (1974) interpreted the unique features of the foraging behavior of gymnotiforms, including active searching and backwards swimming, as being due to tuberous organ mediated electroreception. Blake (1983) examined the kinematics of gymnotiform and notopterid swimming and concluded that these fish are specialized for slow swimming and high maneuverability, and re-emphasized that these fish swim backwards as well as they swim forwards. However, Blake disagreed with Lissmann concerning the evolution of this gymnotiform or anal fin undulatory swimming mode on the basis of two observations. First, in certain mormyrids, such as *Gnathonemus* sp., swimming movements are of the carangiform type, in which the electric organ, being located in the caudal peduncle, is being constantly moved from side-to-side as the fish swims. Secondly, that certain notopterids without an active electroreception exhibit the gymnotiform swimming mode but are visual.

Between the interpretations of Lissmann and Blake, we feel that Lissmann's are more convincing for two reasons:

(1) Both pulse and wave producing species swim similarly. While *Gnathonemus* do not swim in a pure gymnotiform mode, they have a semi-stiff body axis due to the presence of specialized bones, termed Gemminger's bones, that are located along the dorsal and ventral margins of their electric organs (Lissmann 1958) and function to keep their caudal peduncle, and therefore their electric organs, rigid. Moreover, mormyrids can back up. These fish investigate electrically novel items by 'probing motor acts' (Toerring & Belbenoit 1979). In describing the probing motor acts of *Gnathonemus petersii* during discriminatory behaviors, von der Emde (1990) states: 'the fish displayed several lateral tail strokes to the left and to the right while slowly approaching the object backwards'. It is

unlikely that most carangiform swimmers are able to swim backwards with this precision.

(2) Current ideas of gymnotiform evolution suggest that the gymnotiform swimming mode arose after the invention of high-frequency electroreception. If true, this view would support Lissmann's position. In describing the foraging behavior of *Rhabdolichops troscheli*, a morphologically generalized sternopygid gymnotiform, Mago-Leccia & Zaret (1978) state: 'this species was observed to hover approximately 4 cm above the bottom and parallel to it. (...) When several dipteran larvae were dropped within the range of the fish, it moved forward using its anal fin. It captured several of the small prey by the simultaneous rapid sculling of its pectoral fins and opening of its mouth. (...) In contrast, the feeding method of *Eigenmannia virescens* [a derived sternopygid] is to use its anal fin almost exclusively to move forward and backward with equal facility along the bottom of the tank...' Heiligenberg (1973) describes the feeding behavior of *Eigenmannia* as follows: 'When feeding on brine shrimp and other small organisms floating in the water, *Eigenmannia*, particularly when blinded, is commonly seen to catch food near its body wall by backing up and snapping with a quick jerk to the side.' This behavior is almost identical to that described here for *Apteronotus*.

Blake (1983) correctly points out that certain notopterids, such as *Xenomystus* spp., exhibit a gymnotiform swimming mode but possess 'well-developed eyes and lack an [active] electrical sense'. However, having one well developed sensory system does not preclude the development of a second system. Heiligenberg (1973) notes that *Eigenmannia* has good vision and displays a robust oculomotor response, but exhibits an active electrosense. Since Blake's paper, Bullock & Northcutt (1982) have shown that *Xenomystus* is passively electroreceptive. This fact however does not change the correctness of Blake's argument. Passive electroreception, by itself, cannot explain the gymnotiform swimming mode of *Xenomystus*; siluriform catfishes are passively electroreceptive yet swim in a carangiform mode.

In conclusion, gymnotiform swimming, and particularly backwards swimming, is a consistent fea-

ture of high-frequency, waveform electric fishes. In gymnotiforms this behavior may have evolved after the invention of an active electrosense. Only one teleost, the notopterid *Xenomystus nigri*, is known to swim backwards yet does not possess an active electrosense. Therefore, the correlation between backwards swimming and an active electrosense is not absolute, but convincing. This relationship, coupled with the mechanisms of foraging behavior (searching, scanning, and lunging) described here, suggests that swimming backwards is a specialized locomotory mode guided by the constraints introduced by an active electrical sense.

#### Acknowledgements

We are grateful to the following people at the Iowa Lakeside Laboratory who made this project possible. Charles Drewes' wide interest kindled his enthusiasm for videotaping and photographing these fish. Kris Baker composed Figures 1 and 2. Richard Bovbjerg and Robert Cruden, the Lakeside directors, gave us the laboratory space. Ken Lang provided statistical advice. Mark and Judy Wehrspann, the Lakeside Laboratory caretakers, made sure things were in working order. We also thank Joseph Bastian and Walter Heiligenberg for their comments on earlier drafts of this manuscript.

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