

Swimming patterns associated with foraging in phylogenetically and ecologically diverse American weakly electric teleosts (Gymnotiformes)

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Synopsis

The backwards swimming behavior exhibited by American weakly electric fishes (Gymnotiformes) is thought to be an important component of foraging, particularly in the electrolocation of prey items. Previous studies of *Eigenmannia virescens* and *Apteronotus albifrons* have shown that backwards swimming appears to allow a fish to scan a potential prey item across its cutaneous electroreceptor array, then put itself in position for a short, forward lunge preceding ingestion. Adult gymnotiforms exhibit considerable variation in size, shape, and electric organ characteristics. For example, gymnotiforms produce either a wave or a pulse electric organ discharge (EOD). Given this variation, we ask whether the results reported previously can be completely generalized to all gymnotiforms. To address this question we observed the foraging patterns of phylogenetically and ecologically distinct gymnotiforms: three wave species, *E. virescens*, *A. albifrons* and *Sternopygus macrurus*; and three pulse species, *Gymnotus carapo*, *Brachyhypopomus cf. brevirostris*, and *Rhamphichthys rostratus*. Electric organ placement and body shape were also noted in these species to determine if morphological differences correlate with variations in foraging behaviors. Results demonstrate that following prey detection the wave species examined primarily swim backwards during prey approach, prior to lunging forward and ingesting prey. This result is similar to previous findings. In contrast, the pulse species examined detect, approach, and ingest prey primarily in the forward direction, swimming backwards only to reposition themselves.

Introduction

Weakly electric teleosts swim backwards with the same facility that they and other fishes swim forwards. This method of swimming, termed the gymnotiform mode by Breder (1926), is characterized by axial rigidity and is accomplished primarily through anal fin undulation (Blake 1983, Lannoo & Lannoo 1993). Lannoo and Lannoo (1993) examined the foraging patterns of *Apteronotus albifrons* (Siluriformes, Gymnotiformes, Apterontidae [subordinal systematics following Fink & Fink 1996]) and concluded that backwards swimming is an important component of electric fish foraging behavior. In particular, backwards swimming appears to allow a fish to scan a potential

prey item (sensu Lannoo & Lannoo 1993) across its surface electroreceptors, leaving the prey located at or near the mouth and in position for a short, forward lunge prior to ingestion. Given that morphological differences among fish (and other vertebrates) are frequently manifested as behavioral differences (Webb & Blake 1985), as a working hypothesis, we suggest that other gymnotiform species with different electric organ characteristics, and perhaps different morphologies, should exhibit foraging patterns distinct from *A. albifrons* and each other. The present paper is an examination of this hypothesis.

Adult gymnotiform teleosts produce either wave or pulse electric organ discharges (EODs) from electric organs placed along their body, in particular the trunk,

caudal peduncle, and tail, and in some species ventrally near the head (submental organs), such as in *Rhamphichthys rostratus* (Lissmann & Schwassmann 1965, Bass 1986, Heiligenberg 1991). Gymnotiforms emit EOD patterns unique to each species, and in some species, electric organs from different sites on the body produce different EOD patterns (e.g. Bennett & Grundfest 1959, Bass 1986, Heiligenberg 1991, Macadar 1993). Electric organ discharges function in a variety of ways, such as intraspecific communication, object avoidance, and prey detection (Black-Cleworth 1970, Hagedorn 1988, Davis & Hopkins 1988).

Gymnotiforms also vary in body shape from short and relatively deep to elongated and thin; bodies may be compressed or fusiform. For example, *A. albifrons*, like *Eigenmannia virescens*, has a short, compressed body with electric organs positioned caudally along its flanks (Bass 1986). The foraging patterns of these two species have been described previously and are similar (Heiligenberg 1973, Lannoo & Lannoo 1993). The swimming patterns associated with foraging in other gymnotiforms have not been examined. For example, variations in morphology among gymnotiforms include *R. rostratus*, which has a long tube-snout with a terminal mouth and is not likely to feed like *A. albifrons* or *E. virescens*.

Our goal here is threefold: (1) To determine whether foraging behaviors among gymnotiform species vary; (2) because foraging behaviors do vary, to determine whether these differences correspond to variations in swimming patterns, electric organ placement, and body shape; and (3) to provide details of the unusual foraging pattern of *R. rostratus*.

Materials and methods

Animals

We observed six species of South American weakly electric fishes in five families, as follows (phylogeny after Albert & Campos-da-Paz 1998): *Gymnotus carapo* (Gymnotidae); *Rhamphichthys rostratus* (Rhamphichthyidae); *Brachyhyppopomus* cf. *brevirostris* [Hypopomidae (after Albert & Campos-da-Paz 1998, Albert personal communication)]; *Sternopygus macrurus* (Sternopygidae); *Eigenmannia virescens* (Sternopygidae); and *Apteronotus albifrons* (Apteronotidae). The species are available through the commercial pet trade and represent phylogenetic

diversity among gymnotiforms. *Rhamphichthys rostratus* is the only one of the species examined that has a tube-snout, and as we began gathering data we realized that some of the foraging behaviors of this species are unique (see below). We therefore decided to acquire more individuals of *R. rostratus* and observe each animal for a longer period of time.

We purchased four *G. carapo*, twelve *R. rostratus*, nine *B. cf. brevirostris*, two *S. macrurus*, three *E. virescens*, and one *A. albifrons* from tropical fish suppliers. Commercially purchased gymnotiforms often have high parasite loads, and are known to be fragile and difficult to maintain in captivity. We only used healthy, feeding fish for our observations. We kept fish together in two 150 l aquaria on a 12 h light/12 h dark cycle at temperatures from 25°C to 28°C, and maintained them on live blood worms (*Tubifex* sp.). Although we recognize that these different fish species probably feed differently on a variety of prey items, including invertebrates and in some cases small fishes, to reduce the variability in predatory behavior that these various prey would induce, we chose to feed fish a standard prey type (oligochaetes) that would be a component of their natural diet.

Observations

We collected data by feeding and filming each individual in isolation (except *E. virescens* and *A. albifrons*, see below). Films were then edited to include only active feeding bouts; we assembled our data from this set of edited tapes. We quantified key behavioral aspects of foraging and feeding such as prey detection, direction of prey approach, and prey ingestion as follows: we defined prey detection as an event signaled by a change from random searching pattern to directed movement towards a prey item. We then noted distance between the prey and the fish at the point of detection and recorded subsequent direction of prey approach (either backwards or forwards). We defined prey ingestions as instances in which a prey was taken into the oral cavity and not expelled. We recorded the total number of prey ingested for each species. We also noted and counted other unusual behaviors, such as air gulping, barrel-rolls, substrate probing and substrate puffing. In order to quantify feeding behaviors in *A. albifrons*, we reviewed previously taped feeding bouts by Lannoo and Lannoo (1993). We did not quantify behaviors in *E. virescens*.

Filming

We filmed the animals using a JVC SVHS videocassette recorder operated on slow recording speed with Sony SVHS T120 videotapes. An aside: neither the temporal nor spatial resolution of super VHS videotape is sufficient to allow for the detail of fine-scaled motor activity patterns. Videotape is not a substitute for high-speed cinematography, nor does this paper suggest it to be. Nevertheless, as we have previously demonstrated, videotaped feeding sequences adequately permit the repeated observation of key swimming patterns associated with foraging behavior (Lannoo & Lannoo 1993).

We filmed the fish in two different sized tanks: a 12 l tank (30 cm × 15 cm × 15.5 cm) filled to a depth of 2.5 cm with washed and filtered sand (grain size 300 to 600 μm) and a 38 l tank (50 cm × 25 cm × 32 cm) filled to a depth of five cm with washed and filtered sand. We filled each aquarium with aged tap water supplemented with ammonia chloramine remover. Water conductivity in the test tanks varied between 220 and 240 μSiemens cm⁻¹. Total dissolved solids ranged from 1.1 to 1.2 g l⁻¹. At the beginning of each observational period, we bubbled the water in the test tanks to the point of dissolved oxygen saturation prior to introducing the fish. Ambient room light supplemented by a fluorescent lamp positioned over the tank provided the lighting. We taped a metric ruler to the back of the tank to allow an estimation of prey detection distances and swimming rates. We chose tanks for filming that were large enough to allow individual fish to maneuver but small enough to allow the camera full coverage of the tank. Importantly, this approach allowed the resolution of individual prey.

Prior to introducing the fish, we placed 10 to 12 *Tubifex* worms in the filming tank and allowed them 10 min to acclimate, which for many included burrowing into the sand. We then transferred a fish to the filming tank and allowed it 15 min to acclimate. We placed the fluorescent lamp directly over the tank, set the video camera to record, and left the room undisturbed for two hours. We filmed fishes as follows: four *G. carapo* (138 to 221 mm TL [total length], for a total of 18 h); six *R. rostratus* (222 to 281 mm TL, for a total of 108 h); nine *B. cf. brevirostris* (160 mm to 233 TL, for a total of 30 h); and two *S. macrurus* (146 to 160 mm TL, for a total of 10 h). We did not film *E. virescens* and *A. albifrons* in the present study. Instead, we used these animals to confirm the presence and relative frequencies of behaviors reported by Heiligenberg (1973) and

Lannoo and Lannoo (1993) for fishes inhabiting our observational tanks.

We reviewed edited tapes and recorded all foraging behaviors described above. Behaviors recorded and discussed in this paper are either observed or inferred. Examples of observed behaviors include direction of prey approach, prey ingestion, air gulps, rolls, and probes of the substrate. These observed behaviors were quantified as described above. Examples of inferred behavior include scanning and assessing prey as defined in Lannoo and Lannoo (1993) and prey detection. Our primary goal here was to emphasize comparisons across species.

Results

Foraging behaviors common to gymnotiforms

Four behaviors associated with foraging were common to all six species observed. First, gymnotiforms all actively swam about the observation tanks and presumably electrolocated prey (sensu Bastian 1986, Lissmann & Machin 1958); they did not employ sit-and-wait or ambush tactics. Second, individuals of all species were able to swim backwards. Third, backwards swimming was frequently observed as a component of foraging behavior. Fourth, prey were detected in the near field, never more than 4 cm from the body.

Foraging behaviors of Eigenmannia virescens and Aptereronotus albifrons

To review briefly, Lannoo and Lannoo (1993) report that foraging in *A. albifrons* consists of searching for and assessing prey. During searching, locomotion consists of both forward and backward swimming. In its simplest form, searching consists of swimming in a normal, upright position, although *A. albifrons* swim backwards more often than forwards while searching. Once prey detection occurs, *A. albifrons* scan the prey, usually by backwards swimming. *Aptereronotus albifrons* stop swimming backwards when prey is located near the side or the front of the mouth, then lunge forward to capture it. Prey are usually captured by a shallow gape and suck action.

Here, we note that *E. virescens* and *A. albifrons* are compressed fishes of moderate total length with electric organs located along the caudal trunk (Bass 1986). In our observation tanks, prey detection in both species occurred in the near field (up to 2 cm from

Table 1. Comparison of species characteristics and foraging behaviors in a variety of gymnotid fishes. (EOD = electric organ discharge, TL = total length).

Family	Gymnotidae	Rhamphichthyidae	Hypopomidae	Sternopygidae	Apteronotidae
Species (N)	<i>Gymnotus carapo</i> (4)	<i>Rhamphichthys rostratus</i> (12)	<i>Brachyhypopomus cf. brevirostris</i> (9)	<i>Sternopygus macrurus</i> (2)	<i>Apteronotus albifrons</i> (1)
Type of EOD	Pulse	Pulse	Pulse	Wave	Wave
Electric organ location	Trunk	Trunk, Submental	Trunk	Trunk	Trunk
Body shape	Moderate TL, Fusiform	Elongate, Compressed	Moderate TL, Compressed	Moderate TL, Compressed	Moderate TL, Compressed
Direction of swimming after prey detection (% of total prey detected)	Forwards 88.9% (48/54)	Forwards 85.2% (156/183)	Forwards 94.1% (32/34)	Backwards 79.7% (63/79)	Backwards 64.1% (34/53)
Air gulps (h ⁻¹)	82.9	0	18.5	0	0
Other foraging behaviors	Barrel-rolls 90.4 h ⁻¹	Substrate probing 315 h ⁻¹ , Substrate puffing 307 h ⁻¹	Substrate probing 22.6 h ⁻¹	Scanning prey	Scanning prey

their bodies) while swimming either backwards or forwards, followed by a scan accomplished while swimming backwards, and then a lunge forward to ingest the prey (Table 1). These behaviors were identical to those reported by Heiligenberg (1973) and Lannoo & Lannoo (1993), suggesting an insensitivity of these foraging patterns to subtle differences in observational conditions.

Foraging behaviors of *Gymnotus carapo*

Gymnotus carapo have a fusiform body of moderate total length with electric organs located post-cranially along the ventral margin (Bass 1986, Kirschbaum 1995, Unguez & Zakon 1998). In our films, prey detection in *G. carapo* occurred in the near field (within 4 cm of their bodies) and *G. carapo* most often (88.9%) swam forwards to approach these prey (Table 1). However, on at least three occasions, *G. carapo* swam backwards from a resting position to ingest a worm that had surfaced near its trunk. Backwards swimming was frequently observed, however we did not observe scanning as a means of prey assessment, as in *A. albifrons* (Lannoo & Lannoo 1993). Instead, backwards swimming appeared to serve primarily to reposition the animal.

Gymnotus carapo actively fed in short (5–10 min) bouts interspersed between much longer periods of stasis. These fish fed near the substrate and exhibited

other behaviors that differed from *A. albifrons*. For example, *G. carapo* gulped air during feeding (Table 1). Also, *G. carapo* performed quarter-barrel rolls (90°) and swam in short forward spurts along their sides across the bottom of the tank. Rolling in this species has been previously reported as an agonistic behavior (Black-Cleworth 1970). Each of the four fish we observed exhibited this behavior. When rolling, either side of the animal could be used. Unlike the side-searching behavior of *A. albifrons* reported by Lannoo and Lannoo (1993), we could not confirm that the *G. carapo* rolls were associated with foraging. Rolls occurred both during prey detection and approach, and following prey ingestion. It is not clear whether the presence of prey or some other factor related to feeding triggered this behavior. In some instances rolls appeared to be a means of placing the head and mouth in a more favorable position to ingest the prey item.

Foraging behaviors of *Brachyhypopomus cf. brevirostris*

The bodies of *Brachyhypopomus cf. brevirostris* are of moderate total length and compressed, with electric organs placed post-cranially along the ventral margin (Bass 1986, Kirschbaum 1995, Unguez & Zakon 1998). Prey detection in *B. cf. brevirostris* occurred in the near field (within 3 cm of their bodies) and *B. cf. brevirostris* primarily (94%) swam forwards to

approach prey, as did *G. carapo*, but unlike *A. albifrons* (Table 1). *Brachyhypopomus* cf. *brevirostris* swam backwards, but as in *G. carapo*, this behavior appeared to serve primarily as a mode of repositioning the body. Two other behaviors observed in *B. cf. brevirostris* were also seen in *G. carapo*: searching for prey by swimming just above the substrate and swimming to the surface to gulp air. *Brachyhypopomus* cf. *brevirostris* gulped air at a rate about 4.5 times less than in *G. carapo* (Table 1).

Unlike *G. carapo*, *B. cf. brevirostris* probed the substrate. Probing was accomplished by using the anal fin to propel the snout into the substrate. The angle of entry varied from about 45° to nearly vertical. In this species substrate probes were observed a total of 11 times. Three probes involved pushing just the head into the substrate to a depth just past the eyes. Seven probes involved the head and included close to half a body-length. One individual burrowed its body almost completely under the substrate and remained buried for several seconds. This probing behavior may be related to foraging, as is a similar probing behavior observed in *R. rostratus* (see below). But we could not observe buried prey items being captured and never observed prey in the mouths of *B. cf. brevirostris* when they emerged from the substrate. It remains unclear to what extent burrowing functions in searching for and/or seizing prey in this species.

Foraging behaviors of *Sternopygus macrurus*

Sternopygus macrurus have a compressed body of moderate total length with long electric organs placed post-cranially, parallel to the body axis (Bass 1986) and these fish exhibit a foraging pattern similar to *A. albifrons*. In particular, *S. macrurus* tended (80%) to swim forward over a prey item, detect prey in the near field (within 3 cm of their bodies), then swim backwards to pass over it a second time (i.e. scanning) (Table 1). This approach left the prey near the mouth of the fish, allowing ingestion to occur with a slightly downward and forward thrust. Unlike *G. carapo* and *B. cf. brevirostris*, neither air gulps nor substrate probes were observed in this species.

Foraging behaviors of *Rhamphichthys rostratus*

Rhamphichthys rostratus have elongate bodies with two separate electric organ fields: a main electric organ located post-cranially along the ventral margin and a

small submental organ (Bass 1986, Caputi et al. 1994, Kirschbaum 1995, Unguez & Zakon 1998). These two organs differ in the number and spatial distribution of electrocytes and in their innervation patterns, which contribute to differences in the electric organ discharge characteristics between these fields (Caputi et al. 1994). As in *G. carapo* and *B. cf. brevirostris* (and unlike *A. albifrons*, and *S. macrurus*), *R. rostratus* usually approached prey following prey detection in a head on or forward direction (85.2%, Table 1), and used backwards swimming as a means of repositioning their bodies, not for scanning prey items. Unlike *G. carapo*, *R. rostratus* were never observed to swim while rolled onto their sides.

Rhamphichthys rostratus swept their heads back and forth in a zigzag search pattern, but did not detect prey until a prey item was within approximately 1 cm of their mouths. These fish searched in a haphazard pattern using a combination of anal fin and pectoral fin movements to position themselves. The long anal fin was used for forward and backward propulsion, while the two pectoral fins tended to be used for direction changes.

Rhamphichthys rostratus, alone among the gymnotiform fishes observed here, have a long, tube-snout, with the mouth placed terminally. Several behaviors that may be related to the tube-snout morphology were observed in *R. rostratus*. First, substrate probing was observed. As with the probes in *B. cf. brevirostris*, the angle of snout entry into the substrate varied in *R. rostratus* from almost horizontal to almost vertical. All 12 *R. rostratus* we observed probed the substrate. Maximum probing depth appeared to be just behind the eyes. In three instances we observed fish taking prey using this technique. *Rhamphichthys rostratus* also exhibited a variation on snout probing which we termed 'plow-probing,' a behavior in which the snout was forced into the substrate then pushed along while swimming forwards, creating a furrow.

A second unusual behavior associated with foraging in *R. rostratus* was pumping water in and out of their mouths. Expelled water disturbed and displaced the sand substrate. We refer to this behavior as substrate 'puffing.'

Third, prey ingestion combined with probing of the substrate involved the use of forceful suction feeding. The morphology of the *R. rostratus* snout required worms to be ingested from either end; worms grabbed near their midsections were rejected. This initial rejection was usually followed by repeated

ingestion attempts until the worm was grabbed near its end and ingested.

Discussion

Differences in foraging characteristics among gymnotiform fishes

In this study of the foraging characteristics of phylogenetically diverse gymnotiform fish species, certain behaviors were shared, others varied. Among the shared features was the tendency to actively forage for prey. While most freshwater teleosts use sit-and-wait techniques (Zaret 1979), gymnotiforms actively electrolocate prey (see also Lannoo & Lannoo 1993). A second shared feature was the tendency to detect prey only in the near field (within 4 cm).

Although the natural prey of the species observed in this study vary, ranging from fishes in *Gymnotus carapo* and *Sternopygus macrurus* to invertebrates in *Brachyhypopomus* cf. *brevirostris* (Albert personal communication), the standardized use of the same prey consistently elicited interspecific behavioral differences.

Factors that we suspected, a priori, would contribute to variations in foraging patterns were EOD pattern (wave or pulse discharges), electric organ location, and body shape. The component of foraging that we emphasized was the direction fish swam once prey were detected, prior to the final forward swimming lunge. We interpreted backwards swimming near the prey item to be evidence of scanning to assess prey (sensu Lannoo & Lannoo 1993). The direction that fish swam following prey detection and prior to ingestion was independent of electric organ location and body shape, but did correspond well to whether the EOD pattern was pulsed or waveform. Pulse EOD species (*G. carapo*, *B. cf. brevirostris*, *Rhamphichthys rostratus*) tended to swim forwards following prey detection, wave species (*S. macrurus*, *Apteronotus albifrons*) tended to swim backwards following prey detection (Table 1).

Other behavioral differences between species were observed. For example, *G. carapo* and *B. cf. brevirostris* gulped air while foraging; this behavior was never observed in the other species. *Gymnotus carapo* alone performed barrel rolls. *Rhamphichthys rostratus* alone engaged in plow-probes and puffed water at the substrate. *Rhamphichthys rostratus* and *B. cf. brevirostris* probed the substrate, presumably in the process of searching for prey, although the frequency of

substrate probes in *R. rostratus* was about 14 times higher than that observed in *B. cf. brevirostris* (Table 1). The frequency of forward swimming in *R. rostratus* after detecting prey was similar to frequencies in *G. carapo* and *B. cf. brevirostris* but different from frequencies in *S. macrurus* and *A. albifrons* (Table 1).

Backwards swimming

While we were interested by the diversity of behaviors associated with foraging in gymnotiforms, easily the most intriguing result we obtained was the positive correlation between wave species and backwards swimming. According to Lannoo and Lannoo (1993) one function of backwards swimming among gymnotiforms is to scan prey. Scanning allows a fish to assess the prey item by passing the prey over its array of electroreceptors. Scanning may compensate for limitations in image quality due to the lack of an image-focusing mechanism, in the way a lens functions in the visual system (e.g. Heiligenberg 1975). Scanning could theoretically occur by using either forwards or backwards swimming, but backwards swimming scans have the advantage of placing the prey near the head and in position for ingestion.

We did not observe high rates of backwards swimming following prey detection in *G. carapo*, *R. rostratus*, and *B. cf. brevirostris*. We interpret this to mean that scanning is not necessary for assessing prey in gymnotiforms with a pulsed EOD. Although wave discharge rates and pulse discharge rates in gymnotiforms are generally steady (Hagedorn 1988, Macadar 1993, Caputi et al. 1994), pulse rates may be modulated under certain conditions. For example, pulse rate is increased during active swimming periods such as during foraging or at night (Lissmann & Schwassmann 1965). Some pulse species are able to vary or silence their EODs during social interactions (e.g. courtship or territorial aggression, see Black-Cleworth 1970, Hagedorn 1988, Davis & Hopkins 1988). Also, the submental organ in *R. rostratus* contributes to a complex, multi-phasic EOD, which facilitates species-specific recognition (Hopkins & Heiligenberg 1978, Hopkins et al. 1990, Sullivan 1997, Crampton 1998). We were unable to find specific observational or experimental evidence that gymnotiform EODs are modulated during foraging or prey detection. However, von der Emde and Bleckmann (1998) show that when the EODs of mormyrid pulse species were surgically silenced, fishes tended to take longer to search for prey.

Foraging patterns of *Rhamphichthys rostratus*

Although prey items were not frequently observed being ingested following *R. rostratus* substrate probes, it is likely that prey items were successfully taken during a number of these probes, and in three cases we know this to be true. The functional morphology of the tube-shaped buccal structure facilitates extraction of aquatic invertebrates that burrow into or hide within the substrate of the tropical lowland rivers in which these fish are found (Marrero & Winemiller 1993). Marrero and Winemiller (1993) noted that *Stenarchorhynchus curvirostris* (Apterontidae) uses its long snout and terminal mouth to grasp a prey item below the substrate and remove it prior to ingestion. While *S. curvirostris*, *B. cf. brevirostris*, and *R. rostratus* all probe the substrate, only *R. rostratus* has a submental electric organ. We continue to be curious about the possible foraging advantages a submental electric organ could offer fishes that probe their substrate for prey.

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