Acoustic communication in an electric fish, *Pollimyrus isidori* (Mormyridae)*

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**Summary.** It has been known since von Frisch’s work in the 1930’s that mormyrid electric fishes are quite sensitive to sound. We now describe a repertoire of natural sounds produced by the mormyrid, *Pollimyrus isidori*, during breeding and aggression; reception of communication sounds is probably a major function for mormyrid audition.


2. All five sounds are produced primarily at night. Territorial males produce grunts, moans and growls during courtship. Vocalizing is stimulated by the presence of a gravid female on the male’s territory and decreases with the onset of spawning. Hoots and pops are given during agonistic behavior.

3. Grunts are bursts of acoustic pulses, stereotyped for an individual, with the potential as individual signatures.

4. The electric organ is silent during grunts and moans and is discharged at a reduced rate during growls.

5. The courtship and spawning of *Pollimyrus isidori* is described.

**Introduction**

The Mormyridae is a diverse family of African freshwater fishes, of over two hundred species, distinguished by their electrogenic capabilities and highly developed electric sense (reviewed in Hopkins 1986; Bell and Szabo 1986). Like many other teleosts, the mormyrids also exhibit specializations for detecting acoustic signals. In the labyrinth, a small gas bladder coupled to the sacculus probably enhances sensitivity to sound pressure (Stipetic 1939). This anatomy was described over 150 years ago by Heusinger (1826). In contrast to the electric modality, very little is known about biologically significant acoustic signals.

Based on behavioral observations, von Frisch (1938a) concluded that mormyrids were quite sensitive to sound although he did not know the significance of this since he thought the fish’s world to be silent. Since von Frisch, a number of studies have supported and extended his conclusions concerning mormyrid audition (Stipetic 1939; Kramer et al. 1981; McCormick and Popper 1984). The only reported mormyrid sounds are the ‘clicks’ of *Gnathonemus petersii* (Rigley and Marshall 1973), and nothing else is known about the natural acoustic environment of any mormyrid.

Following techniques developed by Birkholtz (1969 and 1970) and by Kirschbaum (1975, 1979, 1982, 1984) for inducing breeding in mormyrids, we have studied breeding behavior in *Pollimyrus isidori*. We have discovered that acoustic signals play a critical role in breeding behavior. In this paper we describe the repertoire of acoustic signals and the breeding and courtship behavior of *Pollimyrus isidori*. A preliminary report of our findings has been published in abstract form (Crawford et al. 1985).

**Materials and methods**

1. **Animals and animal care.** We established a community of 2 male and 3 female *Pollimyrus isidori* (Cuvier and Valenciennes 1846) in a 4801 aquarium (L=183 cm × W=38 cm × H = 54 cm; Fig. 1). Males were distinguished from females by not-
ing the ventral fin margin: males have a concave indentation where the anal fin inserts along the ventral body surface whereas the insertion is straight in females (Iles 1960). Males and females were also distinguished by noting differences in the electric organ discharge (EOD) waveform (Westby and Kirschbaum 1982). The fish were free to swim between five semi-isolated compartments, created by four opaque plastic partitions, but soon adopted preferred areas within the aquarium. Cement cinder blocks and sections of plastic pipe were also provided for shelter. Aquatic vegetation (Ceratopteris thalictroides and Leptodictyum riparium) and filter floss were added for increased heterogeneity and to serve as nesting material. Water temperature was maintained at $27 \pm 2}$ °C. Adult fish were fed on Tubifex worms daily. Larvae were free to graze on algae and zooplankton, and were provided with finely chopped Tubifex. The fish were maintained on a photoperiod regime with 11.5 h light and 11.5 h dark phases separated by 30 min dim white light (‘dawn’) and ‘dusk’ periods. Five 3 W red lights were illuminated behind the aquarium at all times so that during the dark phase there was sufficient light for behavioral observations.

To induce spawning, water conductivity was steadily reduced from about 1,000 $\mu$Mhos/cm to 40 $\mu$Mhos/cm by daily additions of approximately 35 l of deionized water. When aquarium capacity was reached, the water level was decreased by 50%. Rain was simulated by pumping aquarium water through overhead sprinklers for 3 h periods separated by 3 h intervals.

2. Analysis of electric signals. EODs were detected with silver/silver-chloride wire electrodes, amplified with a Grass P-15 differential preamplifier (filter settings: high cut-off $= 50$ kHz, low cut-off $= 0.1$ Hz), and digitized with a Tektronix 5233 digital oscilloscope (1.0 MHz sampling rate). Fast Fourier Transforms of digitized EODs were done on a PDP-11/34 computer using a Digital Equipment Corporation FFT routine.

To facilitate simultaneous behavioral observations and EOD recording in different parts of the aquarium, a permanent electrode was placed in each of its 5 compartments (Fig. 1). A switch outside the aquarium allowed one to select the most appropriate electrode.

3. Analysis of acoustic signals. The sound pressure of acoustic signals was monitored with a pair of calibrated hydrophones (Cesco Transducer Products Model LC-34 and Ceseco pre-amplifiers LG-1344) and further amplified with a Princeton Applied Research amplifier (Model 113; filter settings: low cut-off $= 0.1$ Hz; high cut-off $= 30$ kHz). A Nagra IV-SJ tape recorder was used for recording acoustic signals and for estimating sound pressure levels (SPL); SPL was calculated from readings of the tape recorder's calibrated meter, on the ‘peak’ scale, while a fish produced a sound at a known position. For SPL measurements, a hydrophone was positioned in the middle of section B (Fig. 1) about 12 cm from the bottom; water depth was approximately 35 cm. From this reading, the input to the tape recorder was determined (RMS V) and the output of the hydrophone was calculated. SPL (0 dB referred to 1.0 $\mu$bar $= 0.1$ N/m²) was determined from the calibration curve for the hydrophone. Due to the complex acoustics of aquaria (Parvulescu 1966; Hawkins and Maclennan 1976), the SPLs determined in this way should be taken only as approximations of the SPLs that might be measured at similar distances under natural or free-field conditions.

Signals recorded at 38.1 cm/s were used for sound analysis. Sonograms were made with a Kay Electric Co. Sound Spectrograph (7029A) or with a Spectral-Dynamics 301C spectrum analyzer. Sounds were filtered at 100 to 10,000 Hz and digitized and stored directly on a computer disk, at a sampling rate of 20 kHz using a 12-bit A/D converter. Waveforms were Fourier-analyzed as above. In the complex sound field of the aquarium, sound waveforms undoubtedly depended on the precise location of the fish and hydrophone. Where possible, several examples of recorded waveforms have been provided to illustrate variability.
4. Simultaneous EOD and sound analysis. With an electrode input to one channel of the tape recorder and a hydrophone input to a second, we could record EODs and acoustic signals of a single fish simultaneously. Temporary barriers were used to prevent other fish from approaching the recording site so EOD contamination was minimal. Acoustic contamination was eliminated by selecting nights when only a single animal was vocalizing. Tapes made at 38.1 cm/s were played back at 3.81 cm/s or 1.905 cm/s and displayed on a two channel oscillograph chart recorder (Gould Brush Chart Recorder, Model 220).

5. Behavioral observations. Three sounds (grunts, moans, and growls) were produced by male fish that had been isolated; we never recorded these three sounds from similarly isolated females. The remaining two vocalizations were not heard from isolated animals (see Results). To determine the location of vocalizing fishes, hydrophones were placed at each end of the long aquarium, and by listening in stereo, an observer could determine the end of the tank from which the sound was made (presumably this discrimination was based mainly on intensity cues). We confirmed our ability to locate sound sources by gently tapping the aquarium wall in different places. The identification of vocalizing individuals was reliable since there were just two males vocalizing from opposite ends of the aquarium. Stereo tape recordings, made with the Nagra and analyzed on the real-time spectrum analyzer, confirmed the sound source direction by intensity method.

To correlate vocal behavior with other behaviors, including overt motor patterns, position, and proximity to other fish, we recorded sounds in stereo while coding behavioral data simultaneously on a third track of the tape recorder with a key-operated tone source. Behavioral events were then correlated with ongoing acoustic signals with 1–2 s resolution. Detailed data on courtship maneuvers, egg deposition, and vocal activity were obtained from 9 h of video recorded spawning (AB male, 19 March, 1985).

Individual fish were recognized by natural markings and differences in standard length (SL). The two males were called 'AB' (83 mm SL, 13.5 g) and 'DE' (85 mm SL, 13.4 g) according to the locations of their nesting areas. The three females were named large (82 mm SL, 13.0 g), medium (78 mm SL, 9.9 g), and small (74 mm SL, 7.0 g), according to size.

Results

A. Description of vocalizations

Sounds were first recorded when males AB and DE began building nests within their respective territories (Fig. 1). A rich repertoire of acoustic signals, including 'grunts', 'moans', and 'growls' (Figs. 2 and 3) was heard at night from males stationed on their territories. 'Hoots' and 'pops' were observed only during agonistic encounters (Fig. 4). These vocalizations were relatively infrequent and we have not recorded them from isolated animals. Our behavioral observations of interactions between animals suggest that they are produced by males and females during aggression.

Figure 2 shows a typical sequence of acoustic signals recorded from the AB male. Grunts and growls may be produced singly but sequences beginning with several grunts separated by moans are more common. This sequence terminates with a long growl. Sound pressure levels, at distances of 1–3 cm, were on the order of +28 dB for these three types of vocalizations (Fig. 5).

1. Grunts. Grunts were the most stereotyped of the vocalizations. Lasting approximately 300 ms, they consisted of a series of about 15 pulses of increasing amplitude (Fig. 2B). The pulse repetition rate was approximately 50 Hz. Figure 3A shows examples of single pulses and their power spectra. The peak of the power spectrum was in the 500 to 1000 Hz range. Pulse waveform varied as the fish moved around in the aquarium but was constant from cycle to cycle within a grunt (see consistency in successive pulses in Fig. 3A, 1 and differences between examples 3A, 1–3). Single pulses were followed by a damped oscillation of about 500 Hz in our tank (Fig. 6).

2. Moans. Moans were the most tonal of the five vocalization types. They had a nearly sinusoidal waveform that began softly and steadily increased in amplitude (Figs. 2B and 3B). They varied in duration from 250 ms to about 3 s. The waveform of the moan was also stereotyped from cycle to cycle (Fig. 3B). The sonograms (Fig. 2A) and power spectra (Fig. 3B) reveal two harmonically-related peaks, a fundamental at about 220 Hz and its harmonic at 440 Hz. Many moans were frequency modulated upward or downward by 8–18 Hz. Frequency modulations were examined on real time spectrograms with analysis bandwidth of 3 Hz. Downward sweeps were 2–3 times as common as upward. Direction or presence of frequency modulation did not appear to be dependent upon behavioral context.

3. Growls. Growls, like grunts, were composed of pulses, but each pulse had characteristic ringing waveform, producing a broad spectral peak at about 210 Hz (Fig. 3C). Growls were highly variable in duration with the longest bouts (no silences > 5.0 s) lasting about 40 s and the shortest, less than 2 s. The pulse repetition rate was about 25 Hz or about half that of the grunt (Fig. 3C).

4. Pops. Pops had a sharp onset, very short duration and thus a broad power spectrum (Fig. 4A). These click-like sounds were only heard during fights, chases or other movements involving rapid maneuvers.

5. Hoots. Hoots were the most infrequent sounds and also the most variable (Fig. 4B and C). Hoots
often had a tonal quality with rapid frequency modulation. Figure 4B shows a single 1.0 s burst with a peak power frequency of about 125 Hz. Figure 4C shows a hoot consisting of 4 shorter tonal bursts (each lasting about 200 ms). The waveform plots for several of the bursts in Fig. 4C (2 and 3) reveal a higher frequency, about 200 Hz, than seen in Fig. 4B.

**B. Individual specificity in temporal parameters of vocalizations**

1. **Grunts.** Grunts were highly stereotyped for each of the two males. Male AB produced grunts with a mean pulse rate of 45.3 Hz (\(n=14\), SD = 1.2 Hz) while male DE produced grunts at a mean rate of 54.8 Hz (\(n=14\), SD = 1.8 Hz). The pulse rate
Fig. 4A–C. Sonograms, waveforms and power spectra of pops and hoots. In each example, a sonogram is shown with its digitized waveform below on the same time base. In A and B, part of the waveform is expanded to the right and the corresponding power spectrum is shown. C An amplitude-modulated hoot is shown with its compressed (below) and expanded (right) time domain waveform. Frequency bandwidth, time and frequency resolution for each wide-band sound-spectrogram, A 80–8,000 Hz, 3.3 ms and 300 Hz; B and C 20–2,000 Hz, 13 ms and 75 Hz.
Fig. 5. Sound pressure levels recorded at different distances from fish. Distance estimates were 1–3 cm, 4–6 cm, 7–10 cm, 11–14 cm and 15–20 cm. SPLs were plotted according to the log of the midpoint of each of these ranges. Different vocalization types were displaced slightly along the distance axis for clarity.

![Graph showing sound pressure levels](image)

Distance from Fish (cm)

Fig. 7A. Twenty-four hour periodicity in acoustic behavior. One five-minute sample was taken every 30 min over a 24 h period. The frequency of grunts, moans and growls is shown in A and hoots and pops are shown in B. Vocal activity is primarily restricted to the evening with peaks during dusk and dawn.

![Graph showing time distribution](image)

Fig. 8. Sequence of spawns for males AB and DE and the large female. Each vertical bar indicates a night when the large female spawned with one of the two males. The mean interval between spawns was 17.0 ± 10.6 nights for the large female, 39.5 ± 9.3 nights for male AB, and 31.5 ± 15.7 nights for male DE. The first spawn was observed on 16 December 1984 and the last 27 May 1985 (the animals continued to breed after this last date but the data presented here are based upon this sequence of 10 spawns).

![Waveform graphs](image)

Fig. 6. The pulse repetition rate of the AB male's grunt was 45 Hz, while that of the DE male was 55 Hz. Digitized portions (130 ms) of three different grunts are shown for each male fish, illustrating the high degree of stereotypy in repetition rate for each individual and the consistent difference (dashed lines) between the two animals. Note that each pulse is followed by high frequency oscillations.

![Waveform graphs](image)

Fig. 4. A: Total number of calls. B: Time of day. The frequency of grunts, moans and growls is shown in A and hoots and pops are shown in B. Vocal activity is primarily restricted to the evening with peaks during dusk and dawn.

Sequence of spawns for two males and large female.

- AB: |||||||
- DE: |||||
- LG: |||

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- LG: |||

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- DE: |||||
- LG: |||

![Waveform graphs](image)

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![Waveform graphs](image)
Fig. 9. Heightened vocal activity elicited by the gravid large female. During this continuous 250 s sound spectrogram, the large female swam onto the male's territory twice (dotted lines). The male responded by giving grunts and moans in alternation; we have called these sequences grunt-moan bouts (see Fig. 10). When the female left the territory, males usually terminated grunt-moan bouts and produced growls. This transition to growling is clear in the second trace when the female leaves (second arrow). In the last trace, when the female was on the male’s territory again, the grunt-moan bout seemed to be initiated by the female’s entrance but continued after she left. This was less typical. Real time spectra were made in the 0–3,000 Hz band (frequency and time resolution 30 Hz and 50 ms respectively). The two gaps in the record (lines 1, 3), were inserted to synchronize recording channels. The four clicks at 130 s were room noises.

showed little variability in his grunt pulse repetition rate ($\bar{X} = 55.1$ Hz, SD = 1.2 Hz, n = 14, at 26 °C). Unfortunately we cannot compare rates between males in different aquaria since we do not have the necessary precise temperature data. Grunt duration was more variable than the pulse rate and there was no significant difference between individuals (Student’s $t$-test, $P > 0.05$) (AB male: $310 \pm 58$ ms, n = 14; DE male: $280 \pm 57$ ms, n = 14).

2. Growls. More variability existed in the temporal parameters of growls than grunts. The AB male produced growls with a pulse repetition rate of 25.6 Hz ($n = 12$, SD = 2.4) whereas DE’s growls had a mean rate of 23.0 Hz ($n = 11$, SD = 2.3). Thus the mean pulse rates of the males differed (Student’s $t$-test, $P < 0.02$) but the ranges of pulse rates overlapped. Growl duration (a growling ‘bout’ was defined as a period of growling not interrupted...
C. Behavioral context of vocalizations

1. Twenty-four hour pattern in vocal activity. Vocal activity was much greater at night than during the day. There was a peak in vocal activity at dusk and a second but less pronounced peak at dawn (Fig. 7). The swimming and feeding activity patterns were similar to the vocal activity pattern.

2. Agonistic interactions and territoriality. Figure 1 shows the fish in typical postures and locations within the aquarium. The two males occupied and defended areas at opposite ends of the aquarium, rarely moving into the center section or encountering each other. Males usually swam near the bottom and aggressively chased females from their territories. The largest female also swam close to the bottom. She occupied the central region of the aquarium (section C and the large tube in D). She was the only female that was observed to spawn.

The smaller females were variable in their positions in the aquarium and were restricted to the upper regions of the water column by the other animals. These subordinate females generally hovered within crevices or floating vegetation. They were frequently displaced by rapid chases initiated by males or the large female. Such chases were commonly accompanied by a single pop. We observed several cases with pops in which the chasing fish did not make contact with the subordinate.

The outcomes of chases were scored during 25 different 10 min observation trials. ‘Winners’ aggressively displaced ‘losers’. Since the males were by other vocalizations or silences greater than 5.0 s was 11.2 s (n = 20, SD = 9.7) for male AB and 4.3 s (n = 20, SD = 3.3) for male DE. These measures indicate high variability, and the two males did not differ statistically (Mann-Whitney U-test, U = 229, P > 0.05).

Fig. 11. Vocal activity was elevated during courtship but both males became relatively quiet when spawning began. Bars represent the number of each type of vocalization as a percent of the total number of vocalizations recorded in 44 min. Half of each sample (22 min) was taken during courtship, approximately 4 h before spawning began, and the other half during spawning (the calls of both males have been combined). Data were taken on one night when the DE male spawned (white bars: total number of vocalizations = 630) and on another night when the AB male spawned (black bars: total number of vocalizations = 184). Note that the courtship phase usually occurred early in the night when there was a peak in vocal activity (Fig. 7), even when spawning did not occur. This doubtless contributed to the trend shown here, but the change in vocal activity seen with the onset of spawning was much greater than that seen on non-spawning nights.
on stable non-adjacent territories, they interacted minimally; males frequently displaced females. The smallest female lost every encounter with the two other females; the large breeding female always displaced the smaller females. The dominance relationship amongst the females suggested that rank was determined by size.

We frequently recorded pops and hoots during agonistic interactions between the large female and the territorial males. While on opposite sides of an opaque barrier (e.g., one wall of a plastic tube, see Fig. 1), each fish would lunge, in alternation, toward the barrier as if to approach the fish on the opposite side. Each lunge was accompanied by a pop: sequences of 2 to 6 lunge/pops were heard often and such exchanges commonly terminated with one or two hoots. A lunge typically began with a short dart forward and terminated with a rapid turn. Although the interposed barrier eliminated visual contact between the fishes, they remained in acoustic and electric continuity during these exchanges. These interactions occurred at the male-female territory border and were associated with an increase in EOD rate.

3. Nesting, courtship and spawning. Both males built nests on their territories and vocalized during the nights preceding spawning. On a given spawning night, however, the large female deposited her eggs with only one of the males. The average period of the spawning cycle was 40 days for the AB male and 32 days for the DE male. The large female spawned, on average, every 18 days (Fig. 8).

Early in a male’s breeding cycle he actively patrolled his territory during the evening, and vigorously excluded all females. As the cycle progressed, the frequency of grunts, moans and growls increased. In the middle of the cycle, he began building nests from vegetation and filter floss within spaces provided by tubing and cement structures. Small pieces of nesting material were carried to the nest site in the male’s mouth and forced into confined spaces. Nests were approximately ovoid and about 3 x 3 x 6 cm. Nests from previous spawns were often destroyed and males commonly built 2 new nests (particularly male DE) although only one was used. Nests were always elevated from the bottom by about 5 to 10 cm.

The male’s vocalizing rate steadily increased as the spawning date neared; males usually called from a particular site within their territories. Data on vocalizing as a function of position within the territory were taken on several occasions for each male. The total observation time for males was subdivided into time spent in different sections of the territory. Using data on male position at time of vocalizing, it was then possible to compute rates of sound production in different sections. In two 0.5 h samples taken from each of two males, the rate of vocalizing in the preferred area was about twice that in other regions. Thus, each male tended to vocalize more from one location than from others but did not vocalize exclusively from one area. Over the course of the study, preferred vocalizing areas varied from one breeding cycle to the
next as did nest position. Preferred vocalizing areas were not on the nest site but were generally within 25 cm of the nest. Males did not preferentially vocalize at the borders of their territories.

As the male increased his vocalization rate, he also became increasingly tolerant of the large female; she began to visit his territory more often. Upon entering the territory, she circled above the male several times and left within 10 s of entering. The male often followed her through his territory as she retreated. Such visits were tightly correlated with heightened male vocal activity. The male typically responded to the large female with a long sequence of grunts and moans (a grunt-moan bout) while she was on his territory and then produced a long growl when she swam off the territory (Fig. 9).

The durations of grunt-moan bouts (Fig. 9) averaged 2 to 3 times longer when the large female was on a male's territory compared to when a non-gravid female or no female was present (Fig. 10). This difference was highly significant (Student's t-test, P < 0.0001).

Acoustic signalling reached a peak during the hours preceding spawning, but when spawning began, there was a precipitous drop in the vocal activity of both male fish in the aquarium (Fig. 11), though only one male spawned on a given night (Fig. 8). Spawning was preceded by a period of courtship that lasted as long as 4 hours.

During courtship, the large female repeatedly entered the male's territory and the two engaged in a courtship ritual (Fig. 12A–E). The female swam into the territory above the male (about 15 cm) and the male then approached her from behind. The two engaged in head-to-tail circling (Fig. 12A). From head-to-tail circling, a transition occurred (Fig. 12B) to vent-to-vent coupling (Fig. 12C): the female positioned herself at an oblique angle to the vertical and the male rolled under her so that their ventral surfaces were apposed. In vent-to-vent coupling, the fish appeared to be tightly joined; the couple rotated while quivering (Fig. 12D). The pair then separated (Fig. 12E), and the female swam from the territory. This sequence of events lasted about 10 s and was repeated approximately every 15 min. Occasionally the female left the territory without engaging the male. The male vocalized between interactions, when the female was off his territory, but became quiet when she returned for another courtship ritual.

When spawning began, male vocalizations ceased and interactions on the territory became simplified. Head-to-tail circling, vent-to-vent coupling, quivering were bypassed. The female continued to enter as before and position herself at an oblique angle. The male moved into position against her ventral surface (Fig. 12F). While positioned over the male, the female released a group of 2 to 20 eggs. The female left the territory, the male picked up the eggs in his mouth (Fig. 12G) and deposited them in his nearby nest. Each spawning event, from female entry to departure, lasted only 10–15 s. Spawns occurred for a period of about 6 hours, at intervals of 1 to several min. On two occasions, milky white clouds (presumably sperm released by the male) were observed in the area where the eggs had been deposited.

After spawning, the male patrolled his territory excluding all other fish including his mate. He spent some time close to his nest, gently nudging the nest with his nose and occasionally fanning the nest with his caudal fin. By 24 h, development of the eggs was clearly visible and at 48 h larvae began wiggling within the nest. After 8–10 days,
Fig. 14. Electric organ discharge rates during different acoustic behaviors. A bi-modal sample was analyzed for each male. The overall average rate of EOD was the same for the two males (12 EODs/s) and is plotted as a horizontal line for comparison with rates shown by bars. For both males the rate of EODs was higher than average during acoustically silent periods and much lower than average during each of the three vocalizations. Note that male DE produced no EODs during grunts or moans. A sample 8.76 min in duration was analyzed for male AB, including 37 grunts, 37 moans and 48 growls. A sample 2.72 min in duration was analyzed for male DE, including 14 grunts, 11 moans and 27 growls.

young fish began to disperse from the nest (see also Kirschbaum and Westby 1975; Kirschbaum 1984).

D. Motor correlates of vocalizations

1. Locomotory behaviors and vocalizing. Grunts, moans and growls were all produced during active swimming or hovering. None of these vocalizations was closely associated with any particularly overt motor pattern. The pop was the only sound that was tightly linked to overt motor patterns: aggressive chases and lunges.

2. Electric organ discharge and acoustic vocalizing. Coincident with the onset of breeding under our rain-regime, we noted a sex difference in the EODs of Pollimyrus isidori, confirming Westby and Kirschbaum (1982). The EOD was suppressed when males produced grunts, moans and growls. Figure 13 illustrates the suppression of electric discharges during vocalization. Data from longer records are presented graphically for each male (Fig. 14). Both males produced an average of 12 EOD's per s, but while vocalizing the rate was much lower than this. Inhibition was not as strong during the growl as it was during the other two calls. During silent periods, EODs were produced at a higher rate of about 17 EOD's per s.

Discussion

The electric discharges of mormyroids are well known to subserve social communication (Hopkins 1986) and now we can add vocalizations to the mormyrid repertoire of communication signals. The acoustic repertoire of Pollimyrus isidori includes 5 sounds that can be separated into two categories according to behavioral context: 1) three sounds produced by males in the context of courtship and 2) two sounds produced during agonistic encounters. Although acoustic signaling is seen in many groups of teleosts (Fine et al. 1977; Myrberg 1981; Hawkins and Myrberg 1983), to our knowledge, this is the first report of complex acoustic signaling in mormyrids.

A. Mechanisms of acoustic signal generation and reception

Characteristics of the grunt, moan, and growl suggest a common mechanism for these three vocalizations. These vocalizations are often produced together during a single vocalizing episode and we suggest that they may be produced by a single structure driven by three distinct motor commands. The moan is spectrally quite pure and the waveform is quasi sinusoidal with two main spectral peaks. Moans often grade into, and sometimes out of, growls. The sound spectrograms of these vocalizations are similar (Figs. 2 and 3). Examination of waveforms suggests that the moan is generated by a continuous train of muscle contractions at 220 Hz whereas the growl is generated by short bursts of 220 Hz contractions separated by 40 ms. The grunt could be produced by contractions at 50 Hz acting on the same sonic structure but in a highly damped condition.

It seems likely that, as in many other teleosts, the mormyrid swim bladder is involved in sound production. Orts (1967) has examined the anatomy of the swim bladders of a number of mormyrid species; it occupies 45 to 50% of the volume of the body cavity and a thin sheet of muscle fits around its ventral half. The swim bladder of Pollimyrus isidori might be driven into resonance at 220 Hz to produce the moan. Data from other swim bladder sonic systems show, however, that teleost swimbladders can be driven continuously at frequencies as high as 220 Hz by sonic muscle to produce a moan-like vocalization without resonance (see Tower 1908; Tavolga 1964; Cohen and Winn 1967; Schneider 1967; Tavolga 1971).

It is likely that the inner-ear air bladder-coupled saccular system discussed by von Frisch (1938b) and Stipetic (1939) is critical in reception of the courtship sounds of Pollimyrus isidori (see also Werns and Howland 1976). Recent behavioral audiograms for the mormyrid Gnathonemus peter-
\(sii\) show best sensitivity in the 0.3 to 1.0 kHz range (McCormick and Popper 1984). The match between these data and the acoustic repertoire of *Pollimyrus isidori* is good: all of the sounds for which we were able to make SPL estimates should be at least 30 dB above threshold (at close range) according to the tuning curves of McCormick and Popper (pp. 756; McCormick and Popper 1984).

B. Relationship between electric and acoustic signaling

The only courtship-specific electric behavior we observed in *Pollimyrus isidori* was the cessation of the electric organ during vocalization (Figs. 13 and 14). This contrasts with the wealth of electric signals observed in other species of electric fish (Hopkins 1986; Hopkins and Bass 1981; Hagedorn and Heiligenberg 1985). The significance of the inhibition of EODs during acoustic signals is not yet clear, but suggests interaction at the level of CNS command nuclei for electric and acoustic motor output; the control of sonic and electromotor organs resides in the caudal medulla (Bell et al. 1983). High-frequency bursts of EODs are produced by several species of electric fish and apparently function as courtship displays (Hopkins and Bass 1981; Hagedorn 1986). We have not observed bursts in courting *Pollimyrus isidori*. *Pollimyrus isidori* do, however, exhibit more subtle electrical behaviors such as the preferred latency avoidance or echo responses (Lüker and Kramer 1981), which may be important in courtship. Our analysis of the behavior of free-swimming fish has not allowed us to examine this sort of electrical behavior.

C. Mating behavior and function of acoustic signals

Acoustic signals may allow mormyrids to communicate over longer distances than is possible in the electric modality. Although estimates of the range of electric communication have not yet been made in nature, under free-field conditions, the magnitude of an electric field decays with the cube of distance from a dipole source. This rapid rate of signal attenuation may lead to an effectively short communication range. In the best case, the acoustic signal (SPL) will decay with the inverse first power of distance (under free-field conditions). Acoustic signals may thus be detectable over greater distances, depending on a variety of conditions, including water depth, the nature of the fish as a source (monopolar or dipolar; see Kalmijn 1986), ambient noise and the parameter of the signal to which receivers are sensitive. A comparative analysis of active space (Wilson and Bossert 1963; Brenowitz 1981) in these two modalities is underway.

We suspect that the acoustic signals of territorial males provide distinct conspecifics with information about the presence of and/or location of territories and potential breeding sites. In this sense, we think it is likely that these signals serve as advertisement calls. Play-back experiments point to this sort of function for male vocalization in a number of other teleost fishes (Tavolga 1956; Gerald 1971; Horch and Salmon 1973; Myrberg 1972).

The acoustic signals of *Pollimyrus isidori* may also play a role in individual recognition. We have seen clear differences in temporal parameters of the calls of three male *Pollimyrus isidori*, and these could be used in mate selection by females and/or in inter-male communication. Acoustically-mediated inter-male recognition is known in bicolor damselfish (*Pomacentrus partitus*), although this is probably based on spectral cues (Myrberg and Riggio 1985). Temporal parameters are, however, important in species recognition in damselfish (Myrberg et al. 1978; Spanier 1979) and could serve intraspecific individual recognition in *Pollimyrus isidori*. The variability in pulse repetition rate within the grunts of our individual males was remarkably small, the standard deviation being only 3% of the mean in each case.

Two of our observations indicate that females are the targets of male acoustic signals. First, males dramatically increase the duration of their grunt-moan bouts when a gravid female is nearby (Figs. 9 and 10) and second, males stop vocalizing when they have successfully courted a female to the point of spawning. A related observation is that even the unsuccessful male stops vocalizing when spawning is initiated, suggesting that he is attending to a signal emitted by a member of the spawning pair. The nature of this signal is not yet known.

Of the two sounds heard during aggression, the pop was most closely correlated with lunges and chases. ‘Pops’ and ‘knocking’ sounds have also been reported for other teleosts in aggressive interactions (Dijkgraaf 1947; Myrberg 1972, 1981). It seems possible, as others have suggested (Myrberg 1981; Schwarz 1974; Lanzig 1974), that these sounds might enhance other aspects of aggressive displays. In the male-female interactions we observed in *Pollimyrus isidori*, however, pops were often heard while the individuals were separated by a visually opaque plastic barrier. Possibly the pop augments an electrical display.

Male *Pollimyrus isidori* became highly territorial during breeding. They invested a substantial
amount of time in territorial defense and nest building prior to spawning and continued to defend the territory and tend nests after eggs were deposited. Female parental investment was limited to the production and deposition of ova. Under such conditions in which males make a relatively heavy investment in nesting and parental care, female competition for males is likely (see Emlen and Oring 1977; Li and Owings 1978a). In our laboratory system, there was a great deal of interfemale aggression and all of the eggs laid (in both males nests) were eggs of a single female. This suggests that females were competing for males but this should be confirmed in the field.

D. Conclusion

The courtship sounds of male *Pollimyrus isidori* are among the most elaborate acoustic signals we know of for fish. It is interesting that a fish with a sophisticated electrosensory system has also evolved a relatively complex acoustic repertoire. Considering the physics of signal transmission in the two modalities, acoustic signalling may extend the mormyrid’s communication range or active space.

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