

Novel electrosensory advertising during diurnal resting period in male snoutfish, *Marcusenius altisambesi* (Mormyridae, Teleostei)

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Abstract During the day, weakly electric snoutfish, such as *Marcusenius altisambesi* from the Okavango delta, avoid visually oriented predators by hiding in sheltered, dark places where they discharge their electric organs at a low and variable rate, interspersed with occasional short bursts (mean discharge rate, 4–12 Hz). Hence, histograms of inter-discharge intervals (IDI) are broad and bimodal (IDI range, about 15–500 ms; “variable IDI pattern”). We report here that with a female neighbor in electrical communication reach, captive males of *M. altisambesi* ($N = 4$) each showed a novel type of IDI resting pattern that was characterized by a higher and more constant discharge rate (16–28 Hz). These IDI histograms were unimodal and narrow (IDI range, about 11–100 ms; “regularized IDI pattern”). In each of these males, the regularized pattern vanished when the female neighbors were replaced by males, and the common variable IDI pattern of low rate was observed instead. In an unforced choice paradigm, six *M. altisambesi* experimental females were allowed to choose between two electric fish decoys, one playing back the novel regularized IDI pattern and one playing back the variable IDI pattern. Five experimental females significantly preferred staying close to the decoy playing back the regularized IDI pattern, whereas one female showed the opposite preference. It appears that males advertise to females during their diurnal period of overt inactivity, with an inconspicuous signal that neither threatens conspecifics nor alerts predators by overt behavior. A secondary function of the regularized male IDI pattern could be to advance the reproductive cycle of females.

Keywords Electric organ discharge · Electrocommunication · Reproductive cycle · Sexual attraction · Male advertisement signal · Regularized discharge pattern

Abbreviations

EOD Electric organ discharge
DAM Programmable digital-to-analogue converter with memory
IDI Inter-discharge interval
SL Standard length (tip of upper lip to midbase tail fin)
SID Sharp increase in discharge rate followed by a decrease to the resting level

Introduction

Weakly electric, tropical freshwater fish are known to generate electric organ discharges (EODs) for active electrolocation and communication (reviews, Kramer 1990, 1996; Moller 1995; Bullock et al. 2005; Ladich et al. 2006). Among the African Mormyridae, or snoutfish species, the EOD differs widely in pulse waveform and duration (Hopkins 1988, 1999; Kramer 1996). Within species boundaries, members of the same species vary individually in waveform and pulse duration (Kramer and Westby 1985; Bratton and Kramer 1988). Food-rewarded, trained snoutfish detected these differences in waveform at microsecond resolution (Graff and Kramer 1992; Paintner and Kramer 2003). Snoutfish may thus gain information about the species and individual identity of other individuals, such as sex, age, and readiness for reproduction (review, Kramer 2009).

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In contrast to the EOD waveform, which is stable and does not normally change (except for maturity and reproduction in the males of certain species), the inter-discharge interval (IDI) pattern generated by snoutfish varies greatly with the time of day and the momentary state of excitement (for example, aggression; Bauer 1972). During the day, snoutfish are generally inactive and hide in protected, preferably dark but well aerated places. Many of them are social and hide under crowded conditions, probably because in nature there is competition for good hiding places (B. Kramer, personal observations). To avoid detection from visually oriented predators, snoutfish move and interact very little during the day. It is assumed that the daytime EOD serves a contact-keeping function (Moller 1976).

The diurnal IDI resting pattern was studied in many mormyrid species and was always found to be characterized by a wide range of IDIs and the lowest discharge rate for the species, punctuated by rather regularly occurring short SIDs (sharp rise in discharge rate followed by a decrease to the resting level), as if resetting the EOD rhythm. Histograms generally have two or three modes (Kramer 1990).

We report here for the first time in a mormyrid—captive *Marcusenius altisambesi* males from the Okavango delta—a second type of IDI resting pattern that is regularized and of a higher than usual EOD rate. This was observed when males were in electrical communication reach of a female. Hiding from predators means time lost for fitness-enhancing activities such as foraging, courting, or finding a physiologically suitable territory. Some prey species have found ways to alleviate these costs by adaptive behaviors (Werner et al. 1983; Ferrari and Chivers 2009). The present paper documents the regularized IDI pattern and aims at finding its function.

Materials and methods

Animals and their care

Using a fishing net operated from a small boat, twenty specimens of *Marcusenius altisambesi* Kramer, Skelton, Van der Bank and Wink 2007 were sampled from the Okavango delta, panhandle region, Guma Lagoon (18°57'46.6" S, 22°22'25.3" E), by F.H. van der Bank and B. Kramer, 10–12 August 2004 [permit no: OP46/1C(73) from the Office of the President of Botswana], and exported to the aquarium of Johannesburg University by road (import permit to SA, MPB1537), and to Germany by air (export permit MPE7390; import permit F-13686/04, veterinary border control, Germany; no mortality). In agreement with the CITES convention for endangered species, Washington,

there are no import restrictions for mormyrids to Germany (Z3-27, Bundesamt für Naturschutz, Bonn).

We used ten specimens in the present study. Standard length (SL) of males M1–M4 was 13.7–5.3 cm, that of females F1–F6 ranged from 12.8 to 14.3 cm. Two or three fish of mixed sexes shared one maintenance tank (240 × 50 × 50 cm; water level was 40 cm; water conductivity was about 100 μS/cm; water temperature ranged from 25–27°C; the light/dark regime L:D was 12:12 h). Conditions in experimental tanks were similar (ranges were 25.0 ± 0.1°C, 100 ± 3 μS/cm). Fish received freshly thawed *Chironomus* sp. larvae five times per week, several hours after test sessions. All fish, including those not used in the present study, are presently alive and well in captivity. Regierung der Oberpfalz, Regensburg (provincial government authority), has decreed that it does not issue permits for this type of study (which was observational), but visits labs and animal keeping facilities without notice.

EOD recording and generation

For generating a high resolution EOD suitable for EOD playback, male M1 (Standard length SL, 15.3 cm) was placed head-to-tail between a pair of low-impedance carbon electrodes (at 25°C and 100 μS/cm water conductivity). The potential difference was amplified (Electronics Workshop University of Regensburg, 1–100,000 Hz) and captured by a digital oscilloscope (TDS 420, Tektronix Holland, NV, Heerenveen, The Netherlands, 150 MHz, 1 MΩ input impedance, 250 kHz sampling rate, 11 bit vertical resolution, 2500 points per single sweep) for permanent storage on hard disc.

The biphasic EOD of *M. altisambesi* of about 350 μs pulse duration (Fig. 1) differs little between individual fish (Kramer et al. 2007). The duration of the EOD used for playback in the present study was 339.4 μs as measured within ±2% boundaries of the peak amplitude P, and the Fourier amplitude spectrum is shown in Fig. 1 (EOD centered on the baseline, 2¹³ sampling points, 50 kHz sampling rate, 0.2 Hz frequency resolution; routine provided by software Famos, Berlin, Germany).

For generating an EOD file suitable for playback, a stored EOD was resampled at 500 kHz and 8 bit vertical resolution to meet the requirements of the DAM, a programmable digital-to-analogue converter with memory (Kramer and Weymann 1987).

Recording and analysis of IDI patterns

For recording diurnal IDI resting patterns in pairs of fish, we divided the experimental tank (290 × 70 × 50 cm

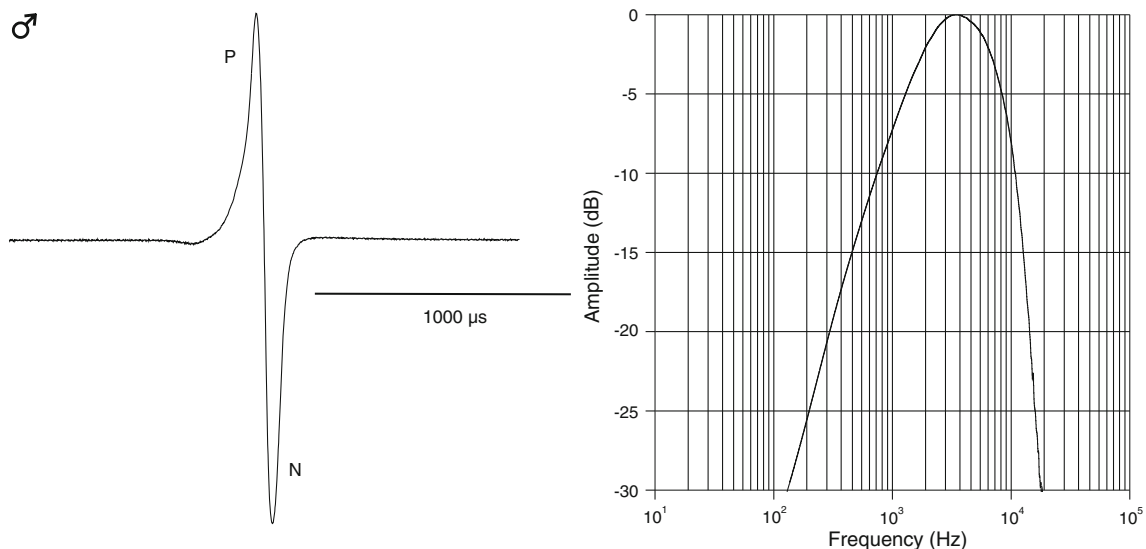


Fig. 1 *Left* Electric organ discharge (EOD) recorded from an *M. altisambesi* (male M1), shown as a graph of voltage over time. Time bar 1000 μs. A head-positive P phase is followed by a negative N phase. *Right* The amplitude spectrum peaks at 3.4 kHz

high; water level, 40 cm) symmetrically into two compartments by plastic wire mesh. For hiding during the day all fish accepted a porous pot. IDI resting patterns, as defined in the present study, were recorded from specimens when resting motionless in their diurnal hiding position for at least 30 s; the only visible movement was breathing. IDI patterns were recorded from four isolated females (F1–F4) and four isolated males (M1–M4) after an acclimatization period of 7 days in the experimental tank. Subsequently, IDI patterns were recorded from four male–male pairs (M1–M2, M1–M3, M2–M4, M3–M4), four female–female pairs (F1–F2, F1–F3, F2–F4, F3–F4), and four mixed male–female pairs (M1–F4, M2–F3, M3–F2, M4–F1). In all cases, the two fish were positioned 50 cm apart, a distance determined to be within mutual electrosensory communication reach (field strength, around 110 μV/cm). Horizontal field strength was measured using a vertically held 1-cm measuring dipole made from glassy carbon electrodes (Sigradur G, HTW, Thierhaupten, Germany; diameter, 1 mm; length, 6 cm; insulated except for the lowest 3 mm; rod separation center-to-center, 1 cm). Maximum field strength was found by rotating the measuring dipole at the site. Each pair of fish was given porous pots. For each condition, three recordings were made within 1 week, with at least 1 day between recordings for the same condition.

A pair of electrodes picked up the EODs of a resting fish. The EODs were differentially amplified (1–100,000 Hz; Electronics Workshop, University of Regensburg) and fed into the analogue-to-digital conversion (ADC) front end of a process computer (Hydra Light, Kinzinger Systeme, Rastadt, Germany), and digitized at 50 kHz sampling rate.

Using an amplitude threshold criterion, a Diadem 8.10 (National Instruments, Austin, Texas, USA) routine generated a list of IDIs that were recorded, displayed, and analyzed.

IDI playback patterns

For playback stimulation, we selected two IDI patterns recorded from male M1 (Fig. 2). The IDI lists generated by the Hydra process computer were reformatted by a routine in QuickBasic to meet DAM requirements, stored on hard disc, and transferred to DAM memory by IEC-bus interface. On PC command, the DAM generated the EOD waveform (shown on Fig. 1) driven by one of the two IDI patterns shown in Fig. 2. Each dipole was driven by one DAM, and both DAM-dipole units were controlled by the same PC.

The IDI pattern of Fig. 2a represents the EOD activity of the selected male when isolated, and Fig. 2b represents the EOD activity when its neighbor fish was a female. The EOD of only one male was selected in order to exclude differences in EOD waveform as a factor in the experiment. These sections of 100 s each were played back in a loop for 50 min per test. Care was taken to choose stop and starting points of the IDI patterns such that transitions were smooth.

The field strength generated by the dipoles was 110 μV/cm at 50 cm distance (porous pot H3 in the center; Fig. 3), 300 μV/cm at 30 cm distance (pots H2 or H4, respectively), and 480 μV/cm at 10 cm distance (pots H1 or H5, respectively). Stimulation dipoles were made from a pair of vertically oriented carbon rods mounted on a horizontally

Fig. 2 Inter-discharge interval (IDI) patterns generated by *M. altisambesi* male M1 while resting during the day. *Left* Sequence of IDIs; *right* histograms of the data to the left. Note geometrically increasing bin width in this and all subsequent histograms, following Graff (1989). **a** Highly variable IDI pattern when male M1 was isolated (mean discharge rate, 6.95 Hz); **b** regularized IDI pattern with a female neighbor in communication reach (mean discharge rate, 17.47 Hz). *N* Total number of IDIs analyzed; modes \pm SE, and minimum and maximum IDIs also shown. Note striking contrast between the two kinds of IDI resting patterns

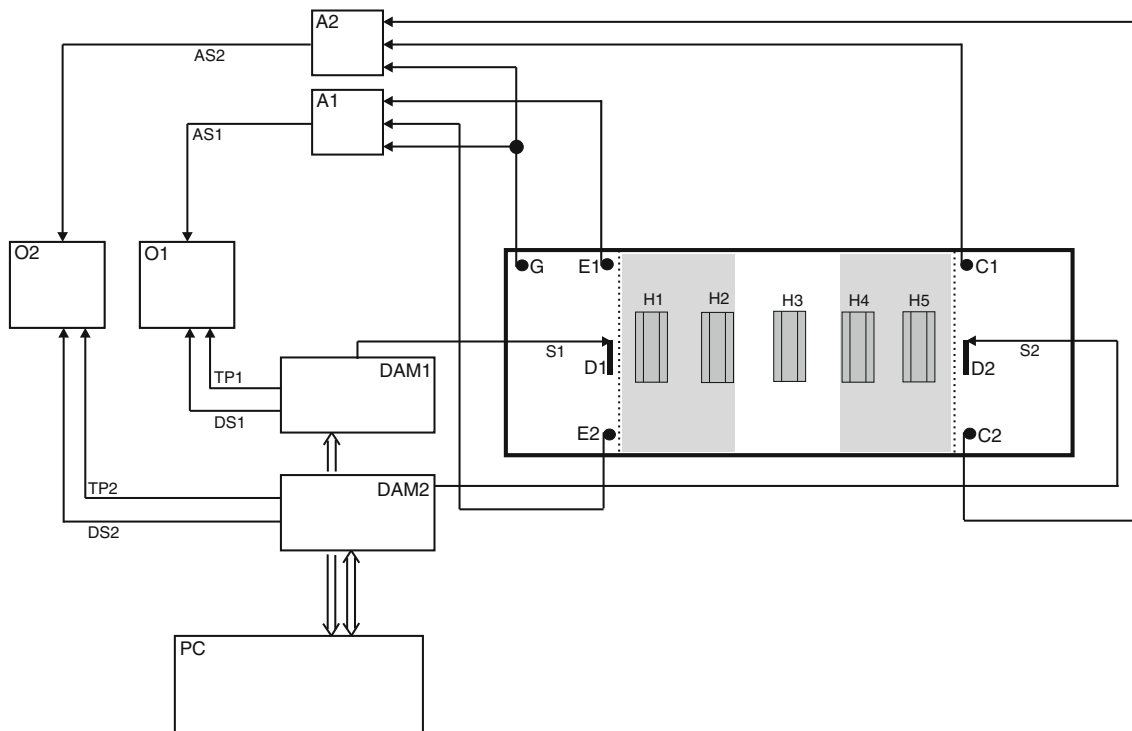
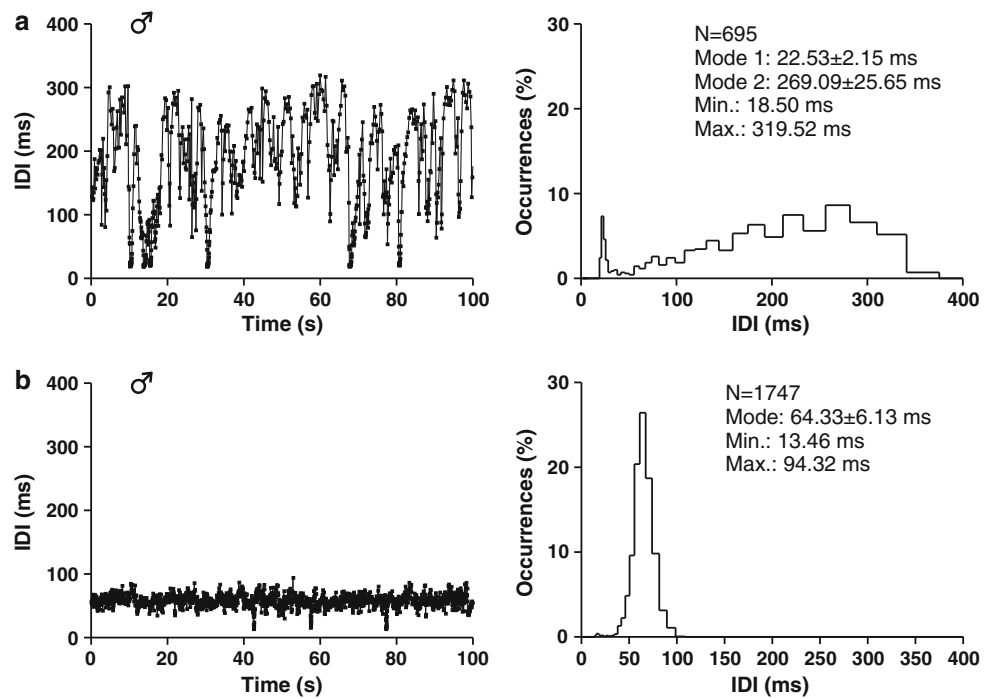


Fig. 3 Setup for playback stimulation with top view of experimental aquarium, equipped with five porous pots for shelter (*H1* to *H5*). The experimental female resides in the center compartment. The two lateral compartments are fenced off with plastic mesh screen behind which electric fish decoys for playback stimulation are positioned. The female can show its preference for one of the two playback patterns by its choice of a pot for residence. Recording and grounding electrodes are shown as *dots*, with *lines* connecting to the electronic

equipment, indicated as follows: *A1*, *A2* differential preamplifier; *AS1*, *AS2* amplified output to oscilloscope; *D1*, *D2* dipoles for playback stimulation; *DAM1*, *DAM2* D/A converter; *DS1*, *DS2* playback pulse to monitoring oscilloscope; *E1*, *E2* and *C1*, *C2* electrode pairs; *G* grounding electrode; *H1*–*H5* porous pots; *O1*, *O2* monitoring oscilloscopes; *PC* personal computer; *S1*, *S2* output signal from D/A converter to dipoles; *TP1*, *TP2* external trigger pulses to oscilloscopes

oriented Plexiglas tube that was kept in position on the aquarium floor by suction cups. The carbon rods of 5 mm diameter and 10 mm height were 3 cm apart and generated the electric field. The output of the DAMs was bipolar and fed into the dipoles directly.

Playback tests

For an unforced choice paradigm, we divided the experimental tank into three compartments with partitions made from plastic screen mesh. Each lateral compartment held an electric fish decoy (a dipole model) placed next to the screen. The central compartment (of 1 m length) held five porous pots placed side by side and spaced at 20 cm intervals; the distance from screen mesh to closest porous pot wall was 10 cm symmetrically on both sides (Fig. 3). The experimental subject was free to choose any one of the five porous pots for its diurnal hiding behavior from the overhead illumination (Mercury vapour lamp for aquaria, type Trocal Super de Luxe HQL 125 W, 1000 lux at the aquarium floor).

There was one 50-min test session per day and 15 repeats per experimental subject on different days. A test session consisted of playback of the EOD shown on Fig. 1 by both dipole models concurrently, driven by two different IDI patterns. When the left dipole played back the variable IDI pattern (shown on Fig. 2a), the right dipole played back the regularized IDI pattern (shown on Fig. 2b), and vice versa. Which dipole was assigned which role was determined by flipping a coin. For subsequent tests with the same experimental subject sides were not changed in order to simulate a territorial neighbor with a fixed hiding position. The first three repeats (days) per experimental subject served for acclimatization and were excluded from data analysis a priori. The experimental subject's hiding position was recorded in terms of time spent in each of the five porous pots it had access to. The time was determined from video recordings with the use of a stop watch; a fish was counted as having entered a pot when half of its length disappeared inside. The first 20 min of a 50-min test session were discarded from data analysis because the initial excitement and restlessness of the experimental subjects made this period unsuitable for analysis (as determined from pilot experiments that were excluded from data analysis in the present study). Association time for a certain dipole and test session was the time an experimental subject spent in one of the two pots close to that dipole during the last 30 min per 50-min test. Mean association time was determined from the last 12 days of a 15-day experimental period. Statistical significance was tested using the software package Prism v4 (with $\alpha = 0.05$, two-sided).

The video equipment consisted of a camera (model FK 6990B-IQ, Cohu, San Diego, CA, USA with zoom lens Pentax/Cosmicar 1.0:8–48 mm, Tokyo, Japan) and a video recorder (Panasonic model AG-7330, S-VHS, HiFi).

Results

IDI patterns

All male *M. altisambesi* of the present study generated the classical variable IDI resting pattern similar to those known from other mormyrid species (Bauer 1974; Kramer 1974, 1990) when isolated and not stimulated by playback, or in the presence of a male neighbor. IDI patterns recorded under these conditions are characterized by low mean discharge rates, a wide range of IDIs with two or three modes, and brief SIDs every few seconds (Fig. 4a, Table 1; Fig. 5b, Table 2). Accordingly, the four *M. altisambesi* males of the present study generated mean discharge rates between 5.81 and 9.6 Hz when isolated, and between 5.73 and 7.69 Hz in male pairs (that is, no notable difference; paired t test: $t_3 = 0.7756$, $P = 0.4945$). Similar mean discharge rates and IDI patterns were observed in the females, independent of whether or not they were isolated (Fig. 4b; Table 1), and independent of the sex of a neighbor if present (Fig. 5a, c; Tables 2, 3). The mean discharge rates generated by isolated females did not differ notably from those of females with a neighbor, either when the neighbor was female (paired t test: $t_3 = 0.8022$, $P = 0.4811$) or male (paired t test: $t_3 = 0.0205$, $P = 0.9850$). A female's discharge rate was also independent of whether a neighbor was male or female (paired t test: $t_3 = 1.532$, $P = 0.2229$).

However, males with a female neighbor generated a novel kind of IDI resting pattern not seen before in any diurnally resting mormyrid. All four males regularized their discharge rate and switched to a higher level than what had been observed in the same males when their neighbor was also of the male sex: mean (\pm SE) discharge rates ranged from 18.49 ± 0.90 to 24.75 ± 1.58 Hz (Figs. 2b, 5c; Table 3; paired t test: $t_3 = 8.653$, $P = 0.0032$). A similar difference was obtained for the comparison of the males' discharge rates when isolated to the same males' rates when paired with a female (paired t test: $t_3 = 8.173$, $P = 0.0038$). The range of IDIs was narrow for the regularized male IDI resting pattern, and histograms were unimodal (mode: about 70 ms). There was a striking contrast between the conventional variable IDI resting pattern of low mean rate and wide IDI range that was punctuated by SIDs every now and then (variable IDI pattern), and the higher discharge rate of the regularized pattern that was stable and monotonous (regularized IDI pattern).

Fig. 4 Diurnal IDI resting patterns recorded from isolated *M. altisambesi* specimens (illustrative figures from individual fish). *Left* Sequence of IDIs over time (s). *Right* Histograms of the data to the left (with statistical summary). **a** Male; **b** female. *N* Total number of IDIs analyzed; modes \pm SE, and minimum and maximum IDIs also shown

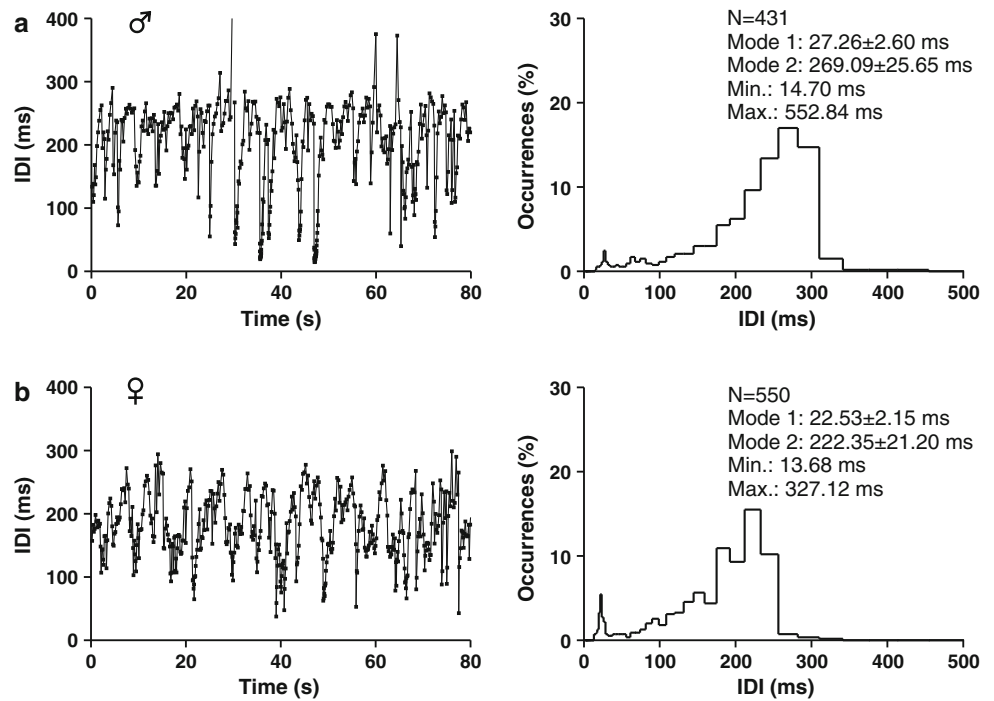
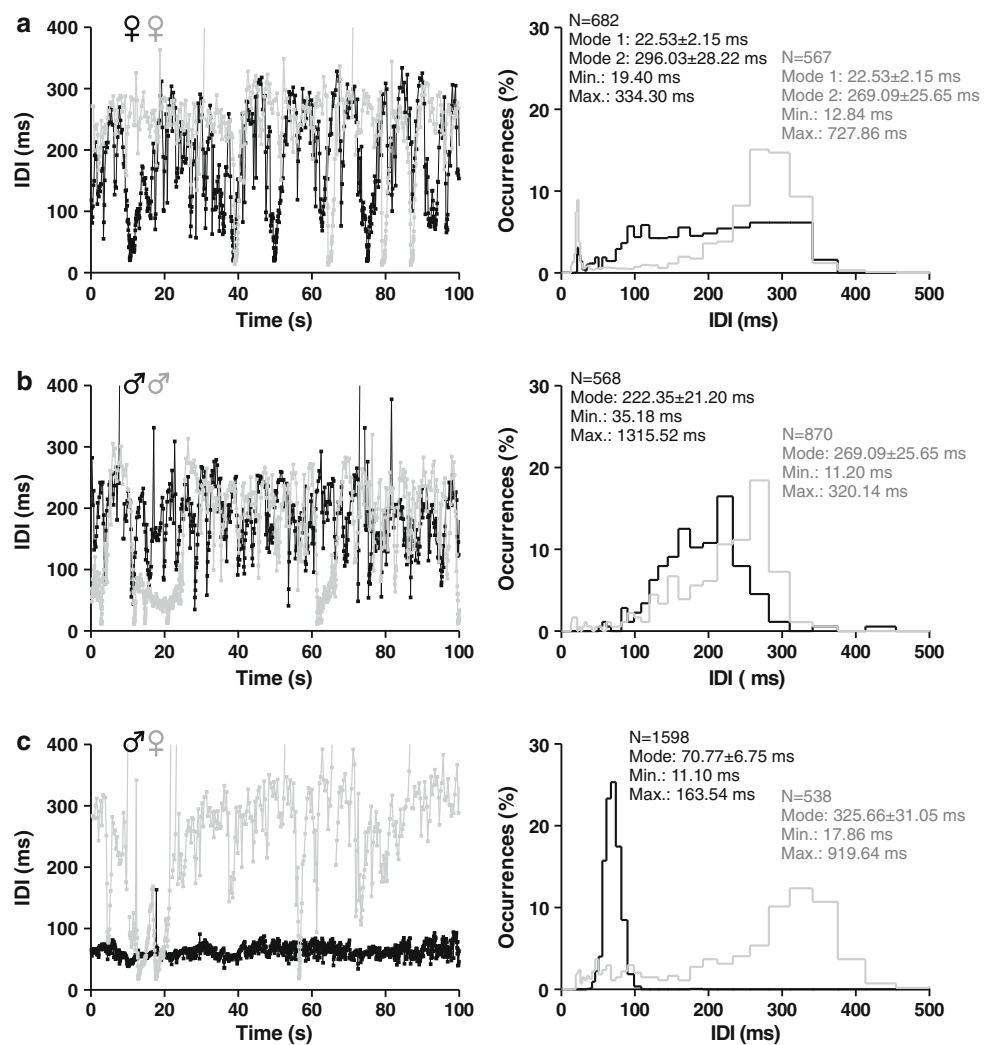


Table 1 Descriptive statistics for the inter-discharge interval patterns recorded from isolated *M. altisambesi* during diurnal resting

Observation	Total duration (s)	I_{min} (ms)	I_{mean} (ms)	I_{max} (ms)	Mean EOD rate (Hz)	Intervals (<i>N</i>)	
Female isolated							
F1	1	50	21.67	118.66	521.01	8.42	421
	2	80	13.68	145.62	327.12	6.88	550
	3	50	17.39	102.50	332.85	10.05	525
F2	1	60	14.72	180.83	315.15	5.53	332
	2	50	14.54	127.55	371.30	7.84	392
	3	50	12.90	93.81	384.51	10.66	533
F3	1	50	12.90	224.71	743.82	4.46	223
	2	50	14.12	231.48	391.91	4.32	216
	3	50	12.71	120.07	314.29	8.06	403
F4	1	60	17.91	181.16	414.16	5.52	331
	2	50	13.36	165.56	1651.51	6.04	302
	3	50	18.88	147.49	491.01	6.78	339
Male isolated							
M1	1	50	17.36	124.38	377.62	8.04	402
	2	50	15.54	118.34	329.67	8.45	422
	3	100	18.50	144.52	319.52	6.95	695
M2	1	50	14.88	138.70	1495.32	7.21	360
	2	60	23.73	89.21	416.65	11.21	673
	3	60	18.95	185.53	1338.40	10.37	622
M3	1	80	14.70	185.28	552.84	5.39	431
	2	50	12.69	146.41	493.02	6.83	341
	3	70	16.42	191.57	320.98	5.22	365
M4	1	50	11.27	141.24	361.11	7.08	354
	2	50	14.71	114.68	514.55	8.72	436
	3	50	13.18	111.61	394.41	8.96	448

I_{min} , I_{max} Shortest and longest interval in IDI pattern, I_{mean} mean interval

Fig. 5 Diurnal IDI resting patterns recorded from isolated *M. altisambesi* specimens (illustrative figures from individual fish). *Left* Sequence of IDIs over time (s). *Right* Histograms of the data to the left (with statistical summary). **a** A pair of females within communication reach (≤ 50 cm), separated by plastic screen mesh; **b** a pair of males within communication reach (≤ 50 cm), separated by plastic screen mesh; **c** a female–male pair within communication reach (≤ 50 cm), separated by plastic screen mesh (female in gray). *N* Total number of IDIs analyzed; modes \pm SE, and minimum and maximum IDIs also shown



Playback tests

Female experimental subjects were exposed to playback of a conspecific EOD (Fig. 1) by two simultaneously active dipoles during the diurnal resting stage, one driven by the variable IDI pattern of Fig. 2a, the other by the regularized IDI pattern shown in Fig. 2b. On stimulus onset, the females responded by leaving their daytime shelter and inspecting the area closest to the active dipoles (which were fenced off by plastic screen mesh). The females moved around the whole space available to them, often switching between sides. Usually the initial excitement wore off quickly and the females retreated into one of the porous pot shelters, however, they changed pots quite often during the remaining playback time.

During the first 2 or 3 days (in one case 7 days) none of the females showed any preference for one of the two IDI patterns. Most of the time they stayed in the center pot, but every now and then they inspected the lateral pots closer to the dipoles. Only after this period did their behavior change:

each one of the six experimental females preferred staying in one of the lateral pots most of the time (example, Fig. 6). Statistical significance was tested for each female individually. Five experimental females associated for a significantly longer time with the dipole that played back the regularized IDI resting pattern (of Fig. 2b) rather than the conventional variable one of Fig. 2a (paired *t* test: $t_{11} > 2.303$, $P < 0.0418$). One experimental female showed the opposite response, that is, it associated for a longer time with the variable pattern than the regularized one (paired *t* test: $t_{11} = 2.831$, $P = 0.0163$, Fig. 7).

Discussion

The observation that certain IDI patterns tend to be similar across mormyrid species has been made repeatedly (Kramer 1990, 1996; Scheffel and Kramer 2000, 2006; Wernerer and Kramer 2002, 2005; Arnegard and Carlson 2005); this is also true for the variable IDI pattern shown when resting

Table 2 Descriptive statistics for the IDI patterns recorded from a diurnally resting pair of *M. altisambesi* of the same sex

	Observation	Total duration (s)	I_{\min} (ms)	I_{mean} (ms)	I_{\max} (ms)	Mean EOD rate (Hz)	Intervals (N)
Male–male pairs							
M1–M2	1	100	35.18	176.40	1315.52	5.68	568
		100	11.20	115.00	320.14	8.70	870
	2	50	16.74	155.28	451.36	6.44	322
		50	18.83	127.71	389.50	7.83	392
	3	50	12.65	180.51	384.12	5.54	277
		50	19.31	175.74	892.03	5.69	285
M1–M3	1	50	14.29	176.68	686.72	5.66	283
		50	12.22	90.74	347.91	11.02	551
	2	100	11.15	211.86	451.55	4.72	472
		100	18.51	170.36	891.11	5.87	587
	3	50	14.32	146.63	299.58	6.82	341
		50	16.98	126.90	314.51	7.88	394
M2–M4	1	30	15.87	180.51	851.11	5.54	166
		30	13.76	187.97	411.67	5.32	160
	2	50	12.24	147.49	391.12	6.78	339
		50	19.43	112.61	351.06	8.88	444
	3	40	17.69	113.38	1986.32	8.82	353
		40	17.36	102.88	1016.10	9.72	389
M3–M4	1	50	18.47	83.89	332.99	11.92	596
		50	26.84	147.28	393.19	6.79	340
	2	40	14.61	147.49	391.34	6.78	271
		40	26.89	230.95	345.23	4.33	173
	3	50	16.19	228.31	412.83	4.38	219
		50	18.47	118.62	418.93	8.43	422
Female–female pairs							
F1–F2	1	50	18.49	179.21	467.29	5.58	279
		50	13.01	156.74	390.37	6.38	319
	2	100	15.13	130.21	300.72	7.68	768
		100	18.05	184.50	411.83	5.42	542
	3	50	14.20	119.90	363.49	8.34	417
		50	17.85	140.85	383.39	7.10	355
F1–F3	1	100	19.40	146.92	334.30	6.82	682
		100	12.84	176.37	727.86	5.67	567
	2	50	21.86	127.23	632.31	7.86	393
		50	19.57	175.13	1011.10	5.71	286
	3	50	15.39	126.58	319.61	7.90	395
		50	17.96	144.09	471.35	6.94	347
F2–F4	1	50	11.45	226.76	315.50	4.41	221
		50	22.50	111.36	611.12	8.98	449
	2	100	17.51	117.79	391.13	8.49	849
		100	13.79	142.86	371.20	7.00	700
	3	50	12.25	165.02	466.91	6.06	303
		50	12.24	143.27	631.05	6.98	349

Table 2 continued

	Observation	Total duration (s)	I_{min} (ms)	I_{mean} (ms)	I_{max} (ms)	Mean EOD rate (Hz)	Intervals (N)
F3–F4	1	50	15.78	191.20	316.89	5.23	262
		50	12.18	179.86	310.41	5.56	278
	2	100	12.23	147.49	817.31	6.78	678
		100	13.94	200.80	516.19	4.98	498
	3	100	11.61	175.44	410.12	5.70	570
		100	15.29	148.81	355.20	6.72	672

I_{min} , I_{max} Shortest and longest interval in IDI pattern, I_{mean} mean interval

Table 3 Descriptive statistics for the IDI patterns recorded from a diurnally resting heterosexual pair of *M. altisambesi*

	Observation	Total duration (s)	I_{min} (ms)	I_{mean} (ms)	I_{max} (ms)	Mean EOD rate (Hz)	Intervals (N)
Male–female pair							
M1–F4	1	100	15.44	51.18	112.34	19.54	1954
		100	13.71	182.48	661.05	5.48	548
	2	100	13.46	57.35	94.32	17.47	1747
		100	17.29	156.49	321.31	6.39	639
	3	100	11.10	51.29	163.54	15.98	1598
		100	17.86	205.30	919.64	5.38	538
M2–F3	1	100	14.18	49.73	151.01	20.11	2011
		100	17.34	231.48	411.31	4.32	432
	2	100	17.16	49.98	99.56	20.01	2001
		100	15.21	200.80	494.72	4.98	498
	3	100	13.19	50.35	70.11	19.86	1986
		100	18.81	217.86	889.51	4.59	459
M3–F2	1	50	14.14	58.51	134.29	17.09	855
		50	17.29	176.68	391.54	5.66	283
	2	100	13.45	49.58	122.41	20.17	2017
		100	14.00	172.12	316.12	5.81	581
	3	100	16.31	54.88	147.87	18.22	1822
		100	15.31	169.20	514.91	5.91	591
M4–F1	1	100	16.61	35.89	89.66	27.86	2786
		100	15.45	97.66	752.51	10.24	1024
	2	100	14.10	42.27	92.47	23.66	2366
		100	10.61	176.06	483.78	5.68	568
	3	100	13.91	44.01	94.33	22.72	2272
		100	13.81	132.98	611.34	7.52	752

I_{min} , I_{max} Shortest and longest interval in IDI pattern, I_{mean} mean interval

during the day. The present study shows for the first time that male snoutfish may generate a second type of diurnal IDI resting pattern, one of a variable instantaneous and very low mean discharge rate that is similar to that shown by females, and long-known from many mormyrid species (review, Kramer 1990); and another, regularized IDI pattern that differs strikingly by its almost constant instantaneous discharge rate that is also two- to threefold higher. Males showed the latter, the regularized IDI pattern, only when their tank neighbor was female, not male. Moreover, five out of six experimental females were attracted by a fish

decoy playing back the regularized IDI pattern rather than the alternative IDI pattern.

One may ask how a male can distinguish between a male and a female neighbor. Pheromonal cues are a possibility but are unknown in snoutfish, perhaps because they have never adequately been looked for. EOD cues are unlikely because the diurnal, highly variable IDI resting pattern of females shows no recognizable difference from that of males, as was also true for EOD waveforms in the present nonbreeding fish. Vocalizations (sound production) have a good chance to turn out to be

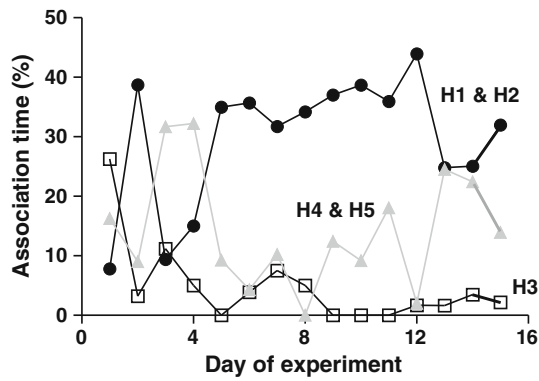


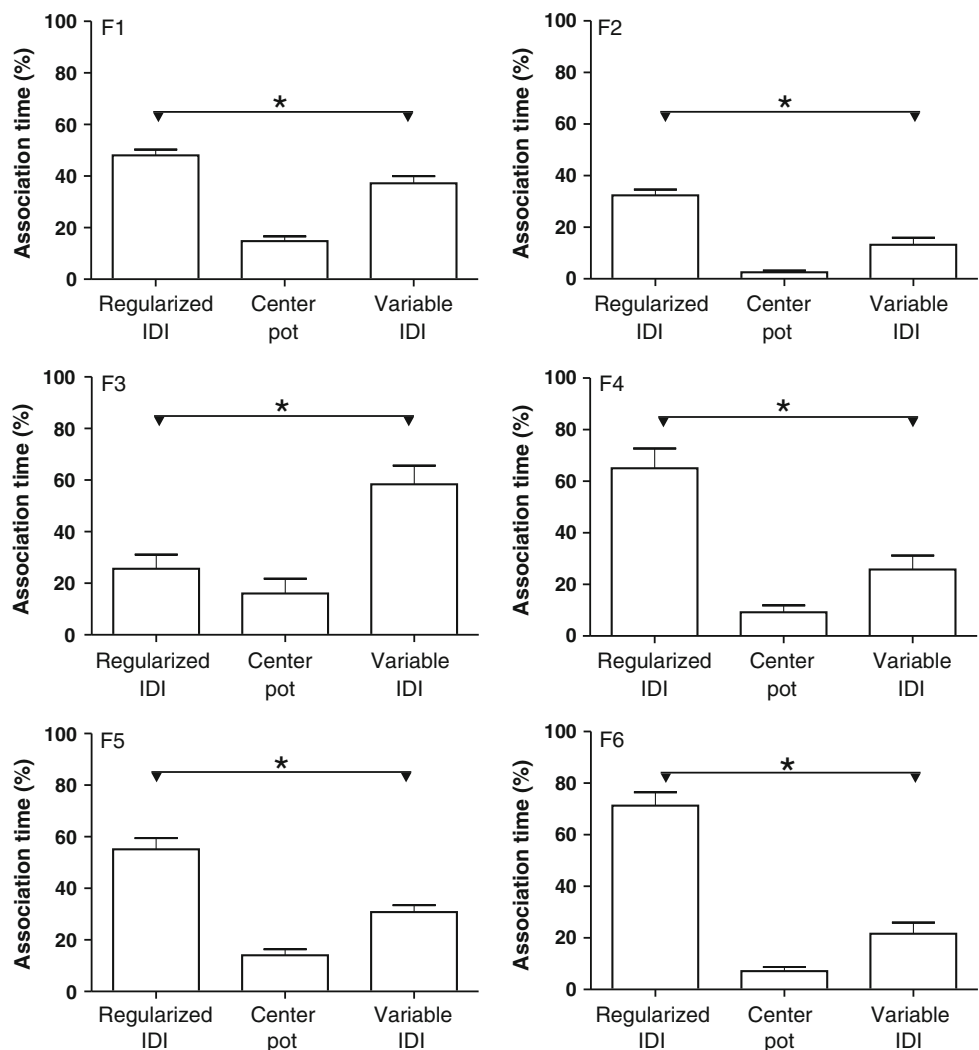
Fig. 6 Association time of representative female experimental subject F2 (as percentage of total playback time per test) as a function of duration of playback experiment in days. *Black dots* Residence of female in porous pots H1 and H2 (those associated with regularized IDI pattern, see Fig. 2); *gray triangles* residence in porous pots H4 and H5 (variable IDI pattern); *squares* residence in porous pot H3 (neutral area of tank)

the relevant cues. *M. altisambesi* males and females generate pulsatile growl and tonal hoot sounds, especially when interacting socially. Females generated fewer growls of shorter duration, longer pulse period (an acoustic feature within a growl), and weaker intensity than males (Lamml and Kramer 2007).

In *Pollimyrus* species, a regularized IDI pattern generated by females was observed during nocturnal courtship and spawning (Bratton and Kramer 1989; Baier and Kramer 2007). The regularized IDI patterns may serve to reduce male aggression, which is very high in *Pollimyrus* males that tend a nest and care for the brood; therefore, appeasement of the male is a prerequisite for female visits.

As far as we can judge, the fish used in the present study were in nonreproductive condition. They seem to be opportunistic breeders, capable of starting gonadal recrudescence (from stage III ova during local ‘winter’ to stage VI ova when spawning) whenever conditions are suitable

Fig. 7 Association time + SE of six female experimental subjects (F1–F6), as shown by their choice of porous pot hiding places during daytime stimulation with two kinds of male IDI resting patterns. Averages over the last 12 days of a 15-day experimental period are shown. *Left columns* present association time with pots close to a dipole playing back the regularized male IDI resting pattern, as opposed to pots close to a dipole playing back a male’s variable IDI resting pattern of low rate (*right columns*). *Center columns* present the time the experimental females spent hiding in the central porous pot (i.e., no choice; shown for information only). Note significant differences between the association times for the two kinds of IDI patterns in all experimental subjects (as indicated by *asterisks*, $P < 0.05$, two-sided). Data do not significantly deviate from normality (D’Agostino and Pearson omnibus normality test, $P > 0.1310$)



in their Okavango floodplain habitat. In males gonadal regression in ‘winter’ appears even less complete and does not happen at all in certain individuals (field study, Kramer 1997). At unpredictable times in our laboratory, several snoutfish species from the same general region, including the South African sibling species *M. pongolensis*, have successfully bred and reared young ones. Rather than time of year, ecological cues such as the (rather unpredictable) arrival of the annual flood from the Angolan mountains seem to be relevant (Merron and Bruton 1995). Among the present group of *M. altisambesi*, courtship and spawning postures have been recorded in our laboratory (Lamml and Kramer 2007). We therefore believe that at least some of our fish may have been in a prereproductive condition.

Why should males court unreceptive females? In his classical experiments, Lehrman (1964) showed that unreceptive female ring doves that were courted by males entered the reproductive cycle earlier than uncourted females, even when separated by a glass screen. Certain female amphibians do not even enter a physiological state of receptivity unless they hear male courtship calls (reviewed in Wilczynski et al. 2005; Cheng 2008). The responses to playback of *M. altisambesi* females that were delayed by 2–3 days seem to point to a similar function of a males’ regularized IDI pattern. Successful advertising during the diurnal period of inactivity could be a male’s best choice to alleviate the high costs from predator pressure, that is, time lost for behaviors that enhance fitness.

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