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Electric Organ Discharges of Mormyrid Fish as a Possible Cue for Predatory Catfish

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Abstract. During reproductive migration the electroreceptive African sharptooth catfish, *Clarias gariepinus* (Siluriformes), preys mainly on a weakly electric fish, the bulldog *Marcusenius macrolepidotus* (Mormyridae; Merron 1993). This is puzzling because the electric organ discharges of known *Marcusenius* species are pulses of a duration (<1 ms) too short for being detected by the catfishes' low-frequency electroreceptive system (optimum sensitivity, 10–30 Hz; Peters and Bretschneider 1981). On the recent discovery that *M. macrolepidotus* males emit discharges lasting approximately ten times longer than those of females (Kramer 1997a) we determined behavioral thresholds for discharges of both sexes, using synthetic playbacks of field-recorded discharges. *C. gariepinus* detected *M. macrolepidotus* male discharges down to a field gradient of 103 $\mu V_{peak\text{-}peak}$/cm and up to a distance of 1.5 m at natural field conditions. In contrast, thresholds for female discharges were not reached with our setup, and we presume the bulldogs eaten by catfish are predominantly male.

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Accentuated male advertisement signals attract more females but also more predators (Ryan et al. 1982; Magnhagen 1991). We found that this phenomenon may explain size-selective predation on a mormyrid fish, as reported from the field (Merron 1993). The mormyridae are a family of weakly electric fish endemic to tropical African freshwaters which use their species-specific electric organ discharges for nocturnal electrocommunication and electrolocation (reviews, Moller 1995; Kramer 1996). The short pulsatile discharges of mormyrids subserve a secretive, nocturnal form of communication that is thought to effectively exclude eavesdropping by predators. However, the widespread African sharptooth catfish, *Clarias gariepinus,* preys mainly on the bulldog, *Marcusenius macrolepidotus*, during reproductive migration, the famous “catfish run” (Bruton 1979; Merron 1993). This species of catfish is electroreceptive (Lissmann and Machin 1963), as are probably all catfishes of the world (Finger et al. 1986; Finger 1986), but its ampullary electroreceptors are sensitive to direct current (DC) and in the very low-frequency range (optimum, 10–30 Hz; Peters and Bretschneider 1981). Therefore *Clarias* spp. are thought to be insensitive to brief electric pulses as generated by most mormyrids.

As only recently discovered, the prey fish *M. macrolepidotus* displays a conspicuous sexual dimorphism in electric organ discharge waveform (Kramer 1997a,b). Around pubescence the discharge duration of male bulldogs increases abruptly up to 11 times the mean duration of juvenile discharges (Kramer 1997a) (Fig. 1). In addition, male discharges develop a marked DC component that increases with discharge duration, and this change in both parameters should facilitate detection by catfish (a discharge had a DC component when its linear voltage mean differed from zero). The aim of the present study was to determine the sensitivity of *C. gariepinus* for electric organ discharges generated by male and female *M. macrolepidotus*, as compared to single-cycle sine-wave pulses of variable duration (Fig. 1).

In food-rewarded training experiments we determined electrosensory thresholds (staircase method as described by Rosenberger 1970) of four *C. gariepinus* for *M. macrolepidotus* discharges of two males and one female (insets, Fig. 1). Two male discharges of different durations were used because of the great variability in male discharge duration observed (Kramer 1997a). Electric organ discharges had been recorded in the field from fish collected at the Upper Zambezi River in Africa (Katima Mulilo, Eastern Caprivi, Namibia; Kramer 1997a,b). The digitally synthesized (Kramer and Weymann 1987) stimuli (amplitude resolution 8 bit; 2048 points per trace; 500 kHz sampling rate) were delivered via an electric dipole fish model (carbon electrodes; rod diameter 0.5 cm, length 1.0 cm, separation 3.0 cm) at a rate of 3 Hz. The dipole generated an electric field closely resembling that of a medium-sized mormyrid fish. The maximum horizontal field gradient our equipment was able to deliver at 35 cm distance, where the trained catfish were resting in a porous pot positioned in parallel to the dipole, was 2.1 $mV_{peak\text{-}peak}$/cm. At 25 cm distance, where the decision point was marked by an open gate, the field gradient was 6.0 $mV_{peak\text{-}peak}$/cm. Artificial, bipolar sine-wave-pulses of variable duration (Fig. 1, inset) were used to determine an equivalent of a frequency-threshold curve for pulselike signals in the catfish. Experiments were performed at field conditions (water temperature, 26±1°C; water conductivity, 100±2 μS/cm). Threshold intensity was defined by 75% or more correct responses of the trained fish.

As predicted from the low-frequency tuning of catfish electroreceptors (Peters and Bretschneider 1981), none of the four trained *C. gariepinus* detected the brief (0.49 ms) female *M. macrolepidotus* discharges, even when using field strengths exceeding that of our largest female (5.1 $mV_{p\text{-}p}$/cm at 25 cm distance; standard length = 13.3 cm). In contrast, all *C. gariepinus* detected the discharges of mature male *M. macrolepidotus* (of both 4.71 ms and 2.43 ms duration), down to field gradients of 103 and 688 $\mu V_{p\text{-}p}$/cm, respectively (Fig. 1). This demonstrates that *C. gariepinus* is at least one order of magnitude less sensitive to female than to male discharges of long duration. Bipolar sine-wave pulses of 4 ms and 2 ms duration were detected down to 339 and 1047 $\mu V_{p\text{-}p}$/cm. Following a power function with negative exponent, thresholds for sine-wave pulses de-

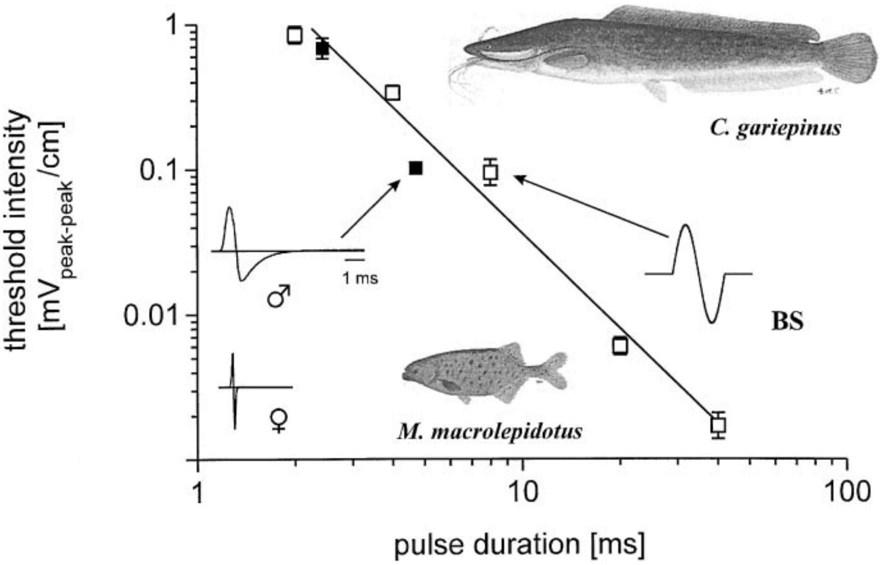

Fig. 1. Comparison of electrosensory thresholds in *Clarias gariepinus* for the electric organ discharges of *Marcusenius macrolepidotus* males, with thresholds for bipolar, single-cycle sine-wave pulses of variable duration (means ± SD). ■, Discharges of *M. macrolepidotus* males (of 2.43 or 4.71 ms duration, the latter discharge shown in inset); □, bipolar sine-wave pulses (BS). Least-squares regression line shown for bipolar sine-wave pulses. Note close agreement between thresholds for male discharges and bipolar sine-wave pulses. Thresholds for discharges of a *M. macrolepidotus* female (*inset*, ♀) were beyond 6.0 $mV_{p\text{-}p}$/cm, that is, above the field strength generated by our largest female (5.1 $mV_{p\text{-}p}$/cm; SL = 13.3 cm), both measured at a distance of 25 cm, and were not reached with our setup. Identical time bar for all insets. (Fish pictures from Skelton 1993)

creased with increasing duration (straight line in a log-log plot with a slope of –0.97 $mV_{p\text{-}p} \cdot ms/cm$). There was close agreement between thresholds for male discharges and bipolar sine-wave pulses of similar duration (see Fig. 1). However, in sine-wave pulses a DC content is totally lacking, and the bulldog discharge of long duration was detected at an even lower threshold than a sine-wave pulse of the same duration (unpaired t-test, $P<0.0001$, $t=13.86$, $df=18$, $n=10$ in each sample).

The distance *C. gariepinus* ($n=4$) detects male *M. macrolepidotus* discharges depends on several factors, such as signal source amplitude that increases with the size of an electric fish, and discharge duration. At realistic field conditions (26° C, 100 µS/cm) the distance is up to 1.5 m. This is a surprisingly large reach for nonspecialized but extremely sensitive ampullary electroreceptors such as those of catfish. In intraspecific electric communication a similar reach was observed in the mormyrid *Brienomyrus niger* (Squire and Moller 1989), relying on its tuberous Knollenorgan receptors that are coadapted to the species-specific electric organ discharge.

Clearly a male bulldog's "handicap" of being detected by a catfish increases with discharge duration and strength of DC component that may be positively correlated with reproductive success. Males with a superior handicap would have a mating advantage but no survival advantage, the latter seen in a field study (Kramer 1997a,b): discharges of the longest duration were observed only in some of the smaller males that had just become sexually mature, suggesting predation pressure and lower survival rates of males with the most accentuated malelike discharges (Kramer 1997a).

Chemoreception is generally thought to play the major role in prey detection in catfish (Hara 1992); in *C. gariepinus*, however, electroreception seems to be of similar importance. In addition to detecting DC fields that all prey emit, *C. gariepinus* also detects the electric organ discharges of male *M. macrolepidotus* so that it can feast on this species shortly before reproduction.

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