SOUND PRODUCTION IN THE TERRITORIAL BEHAVIOUR OF THE CHURCHILL *PETROCEPHALUS CATOSTOMA* (MORMYRIDAE, TELEOSTEI) FROM THE UPPER ZAMBEZI RIVER

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ABSTRACT

This is the first description of vocalisations produced by the mormyrid species *Petrocephalus catostoma* from the Upper Zambezi River whilst defending a territory. Agonistic behavioural displays of a dominant male towards a conspecific, such as mutual circling or short attacks, were accompanied by characteristic tonal sounds, termed hoots. The mean hoot duration (43 ± SD 1.8 ms) was longer, and the fundamental frequency (H1, 180 ± SD 4.7 Hz) lower, than in the closely related species *Petrocephalus ballayi*. *P. catostoma* vocalised hoots only during intraspecific agonistic interactions, especially those accompanying territorial conflict.

Key words: aggression, electric fish, sound production, territory, vocalisation

INTRODUCTION

Many fish species produce elaborate vocalisations during reproductive behaviour or territorial defence (Amorim 2006) that have been shown to function as signals in many cases (Ladich 2004). The African snoutfishes are well known for their electric sense, used for object location (Von der Emde & Schwarz 2002) and communication (reviews, Moller 1995, Kramer 1996). Moreover, communication by acoustic signals seems more widespread within this fish family than known until recently (review, Crawford 1997). Recent observations document sound production not only in several species of the "strongly acoustic" genus *Pollimyrus* that vocalise species-specific courtship songs (Crawford et al. 1986, 1997a,b; Lamml & Kramer 2005, 2006), but also in three allopatric populations within the *Marcusenius macrolepidotus* species

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complex (Lamml & Kramer 2007) that have now been recognised as distinct species (Kramer et al. 2007). Within the genus *Petrocephalus* up to now only the species *Petrocephalus ballayi* from Lake Tumba (equatorial region of Zaire) was known to vocalise (Crawford 1997). Here we document vocalisations accompanying agonistic interactions by another mormyrid species, *Petrocephalus catostoma*, commonly known as the Churchill, from the Upper Zambezi River (see Kramer & Van der Bank 2000 for a detailed description of this form of *P. catostoma*). A more thorough critical revision of the allopatric populations of *P. catostoma* is underway (Kramer *et al.*, in preparation).

METHODS

Twelve *Petrocephalus catostoma* (Günther, 1866) (Figure 1) were caught in August 1994 in the Upper Zambezi River near Katima Mulilo (17°29´20´´S, 24°16´18´´E, Namibia) and transported to the laboratory in Regensburg, Germany, by air. For the present study, we observed six males and one female [standard lengths (SL), 9.1-10.4 cm]. Two males and one female were kept together in a 360-litre aquarium with an external filter (Eheim model 2213). Stones and plants (*Cryptocoryne affinis* and *Vesicularia dubyana*) were offered for shelter. Water temperature was adjusted to 25°C, and the L:D cycle was 12:12 hours. Animals were fed on chironomid larvae five times per week. Additional observations of two pairs of

Figure 1. Photograph of a *P. catostoma* male (9.2 cm SL) from the Upper Zambezi River. Specimens have a uniform silver-grey coloration. (SL = distance tip of snout to midbase of caudal fin).

male *P. catostoma* were made under similar conditions but for an opaque plastic partition separating the highly aggressive fish from one another. In both ♂♂ pairs we removed the partition immediately before the nocturnal observational period to allow the fish to show their unrestrained behaviour.

Fish behaviour was videotaped (Panasonic AG-7330 videorecorder, Hifi, S-VHS) during the daily feeding period shortly before dark in the ♂♂♀ group and during dark in both ♂♂ pairs, using infrared illumination with no visible light (model UF 500 FL, Derwent Systems, Cramlington, UK, λ ≥ 800 nm) and an infrared-sensitive camera (model FK 6990-IQ, Cohu, San Diego, CA, USA). Simultaneously, we recorded sounds with a hydrophone (Brüel & Kjær, Model 8101, 1-125,000 Hz frequency response), positioned near the common territory boundary. Sounds were amplified with a measuring amplifier (Brüel & Kjær, Model 2610, 2-200,000 Hz frequency response) and recorded on the audio-track of the video-recorder. To reduce low frequency noise, the amplified hydrophone output was bandpass-filtered (40 Hz to 10 000 Hz passband, linear phase response, -24 dB attenuation/ octave) using an electronic filter (Wavetek-Rockland, Model 452). Vocalisations were digitised at 48 kHz sampling rate and 16 bit resolution using the standard soundcard of an IBM-compatible computer (Pentium IV, 1.7 GHz), controlled by the software Avisoft-SASLabPro Version 4.33 (Avisoft, Bioacoustics, Berlin, Germany).

The animals vocalised only at a close distance from each other. Therefore, we were unable to assign vocalisations to a specific individual of a pair. To evaluate sound duration and number of sound pulses, we used the cursor and zoom-functions of Avisoft. Frequency parameters, such as fundamental frequency (H1), frequency of strongest intensity (peak-amplitude frequency, PAF) and frequency of additional harmonics, were estimated from amplitude spectra generated using Avisoft routines. Given the short duration of the hoot, the entire sound was used for the generation of amplitude spectra (frequency resolution: 1.46 - 2.9 Hz). Due to the downward frequency modulation observed during a hoot, the harmonics are wider than the theoretical spectral lines (Fig. 2C). This effect, however, is less prominent for the first few harmonics that are presumably the more relevant ones. Hoot pulse period was measured by visually estimating the period between adjacent peaks of hoot pulses. We excluded overlapping hoots from the analysis. To determine the absolute sound pressure level (SPL) of vocalisations generated at about 10 cm distance from the hydrophone we read the relative SPL off the measuring amplifier and calculated the absolute values (dB re: 1 µPa) based on the sensitivity of the hydrophone.

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RESULTS

Two male and one female *P. catostoma* that had been kept together in the same aquarium for months showed strong territoriality and defended stable territories, as described in detail by Scheffel (2006) for the same individuals. During the daily feeding period an individual (the subdominant male or the female) sometimes ventured into the dominant male's territory in pursuit of an extra chironomid larvae. The dominant male aggressively chased away both invaders from his territory. Territory defence behaviour at the common border consisted of mutual circling, alternating with short, darting attacks of the dominant male against his opponent. It was during these agonistic interactions that we recorded short sounds of tonal quality, so-called hoots (Figure 2, term adopted from Crawford et al. 1986 for *Pollimyrus adspersus*). These observations of aggressive encounters in the ♂♂♀ group were very similar to those observed in the ♂♂ pairs when individuals approached one another. In both settings, territorial disputes led to intense fighting correlated with many hoot sounds.

Hoots are very loud sounds, and, in a quiet environment, are audible to a human listener without any electronic gear (absolute SPL about 135 dB re: 1 µPa at a hydrophone-fish distance of about 10 cm). Figure 2 shows a typical hoot and its acoustic characteristics. The hoot oscillogram displays a short burst consisting of 4-16 strong acoustic pulses separated by weak sinusoidal oscillations (Figure 2A-A') with a mean total hoot duration of 43 ± SD 1.8 ms. Hoots showed spectral energy from about 100 Hz to more than 2000 Hz distributed over several harmonics (sonogram in Figure 2B). The fundamental frequency (H1) at a mean 180 ± SD 4.7 Hz was not always the component of strongest intensity (PAF, see amplitude spectrum in Figure 2C). Additional harmonics occurred at 358 ± SD 9.2 Hz (H2), 543 ± SD 17.1 Hz (H3), and at higher frequencies. Table 1 summarises the characteristics of the hoot sounds produced by the three groups of fish.

DISCUSSION

The present observations clearly demonstrate sound production in yet another mormyrid species, *Petrocephalus catostoma* from the Upper Zambezi River, during agonistic interactions. The mormyrid species *Pollimyrus adspersus* (Crawford et al. 1986), *Pollimyrus isidori* (Crawford et al. 1997a), *Petrocephalus ballayi* (Crawford 1997), and *Marcusenius cf. macrolepidotus* (Lamml & Kramer 2007), representing, in addition to *M. macrolepidotus,* the new species *M. altisambesi* and the resurrected species *M. pongolensis* (recognised by Kramer et al. 2007), generate similar tonal sounds of short duration, termed hoots, during agonistic encounters.
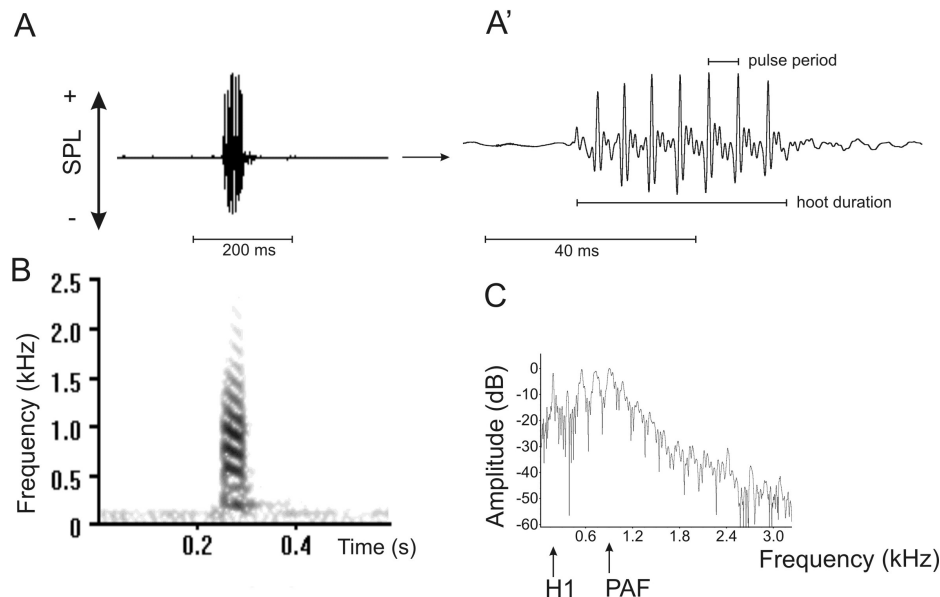
Figure 2. Temporal and spectral characteristics of the hoot. (A-A') Oscillogram of a hoot at low and high temporal resolution. (B) Sonogram (frequency resolution, 20 Hz; temporal resolution, 3.2 ms) and (C) amplitude spectrum for the same hoot. Note the multi-harmonic spectral structure. The frequency of strongest intensity (PAF) at 910 Hz corresponds approximately to the 5th harmonic in this particular hoot (H1 at 187 Hz in the hoot shown). Amplitude spectrum: frequency resolution 2.9 Hz.

Many fish species generate sounds during competitive feeding, for example the grey gurnard, *Eutrigla gurnardus* (Amorim et. al. 2004). The ♂♂♀ group of the present paper produced many hoots during agonistic encounters when being fed. By contrast, the ♂♂ *P. catostoma* pairs produced hoots during interactions that were correlated with agonistic territorial behaviour rather than feeding, an ethological context that had already been suggested for the hoots of *P. ballayi* by Crawford (1997).

Both *P. catostoma* and *P. ballayi* hoots are much louder (135 dB re: 1 μPa in *P. catostoma*; 130 dB re: 1 μPa in *P. ballayi*) than those of the other mormyrid species (e.g. 109 dB re: 1 μPa in three *M. macrolepidotus*-complex species Lamml & Kramer 2007*)*. Moreover, *P. catostoma* hoots differed from those of its congener *P. ballayi* by their longer duration (mean 43 ± SD 1.8 ms vs. 30 ms; SD not given) and their lower first harmonic (180 ± SD 4.7 Hz vs. 215 ± 21 Hz). Additionally, up to three harmonics were present in *P. ballayi* hoots (Crawford 1997) whereas the hoots of *P. catostoma* exhibited a multi-harmonic spectral distribution. The mechanism of sound production

TABLE 1

Hoot characteristics of *P. catostoma* from the Upper Zambezi River. N=10 vocalisa-
tions during agonistic interactions within one ♂♂♀ group and in two ♂♂ pairs.
All sounds were passband-filtered at 40 Hz-10 000 Hz. Water temperature:
24.4–25.2 ºC. H1, first harmonic or fundamental, H2, second harmonic, etc.

	Hoot duration (ms)	PAF (Hz)	H1 (Hz)	H2 (Hz)	H3 (Hz)	Number of acoustic pulses* per hoot	Pulse period (ms)
Male 1 (9.6 cm SL)							
Male 2 (10.1 cm SL)							
Female 1 (10.4 cm SL)							
Mean/ Median*	45.3	185	185	368	559	6.5*	5.28
Minimum	22.8	176	176	346	542	4	5.2
Maximum	74.5	193	193	398	585	16	5.5
Standard deviation (SD)	16.9	6.5	6.5	15.8	14.8	2.75*	0.13
Male 3 (9.1 cm SL)							
Male 4 (9.3 cm SL)							
Mean/ Median*	44.5	416	175	349	525	7.5*	5.7
Minimum	33.2	161	161	333	499	6	5
Maximum	54.6	674	197	379	576	9	5.95
Standard deviation (SD)	8.06	161	12.6	18.6	29.6	1.0*	0.35
Male 5 (9.8 cm SL)							
Male 6 (9.2 cm SL)							
Mean/ Median*	41.7	436	181	358	544	8.0*	5.4
Minimum	33.4	176	176	352	525	6	5.2
Maximum	57.1	930	187	364	569	11	5.7
Standard deviation (SD)	6.5	304	4.9	4.7	13.3	0.5*	0.14

* Median and semi-interquartile ranges for count measures.

in *P. catostoma* is unknown. However, the sound structure seems
to point to an extremely fast swimbladder drumming mechanism as
demonstrated for the courtship songs of male *Pollimyrus adspersus*
by Crawford & Huang (1999). Differences either in body size or in
the sound generating or resonant structures might be the proximate
cause for the frequency differences between the two *Petrocephalus*
species.

The signal value of hoots is unstudied at present, but it is clear
that in *P. catostoma* hoots accompany threatening behaviour. It is
unknown at present whether or not EOD production is arrested during
hoot vocalisations, as observed in two parapatric Dwarf Stonebasher
species, *Pollimyrus castelnaui* and *P. marianne,* when vocalising their

long courtship songs (Baier & Kramer 2007). *Petrocephalus* is a basal clade within the family Mormyridae and our observation strengthens the view of vocalisation representing a plesiomorphic trait for this family. A growing number of mormyrids discovered vocalising during intense social behaviours indicate that we are bound for more important discoveries in the communication of this group of weakly electric fish.

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