SOUND PRODUCTION IN THE REPRODUCTIVE BEHAVIOUR OF THE WEAKLY ELECTRIC FISH *POLLIMYRUS MARIANNE* KRAMER ET AL. 2003 (MORMYRIDAE, TELEOSTEI)

MICHAEL LAMML* AND BERND KRAMER

Zoological Institute of the University of Regensburg, D-93040 Regensburg, Germany

ABSTRACT

In addition to their electric organ discharges, two West African mormyrid species are known to generate sounds during reproduction. Here, we document the reproductive behaviour and concurrent vocalisations recorded in captive specimens of the new species *Pollimyrus marianne* from the Upper Zambezi River. Prior to spawning, three male *P. marianne* established a territory and built a nest of filamentous plant material each (that would hold eggs and larvae at a later stage). Beginning with territory establishment and usually at night, only the males generated two distinct vocalisations, a tonal moan (average duration, 2.26 ± SD 0.6 s), and a harsh grunt (0.596 ± SD 0.029 s; grunt pulse repetition rate, PRR, 32.1 ± SD 1.24 Hz at 25.4 ± SD 0.15 °C). Both vocalisation types were similar to, but clearly different from, those recorded in the two West African species, *P. isidori* and *P. adspersus,* the PRR (Pulse Repetition Rate) of which were higher by 25% and 60%, respectively (at similar temperature). At constant standard length, some of a male *P. marianne's* sound characteristics varied only slightly over two years, but depended clearly on water temperature. When no other fish were present, the three males produced moans only sporadically. When, however, females were visiting, the males generated long-lasting moan sequences that were superimposed by grunts (moan-grunt bouts; average duration, 14.69 ± SD 2.2 s). The maximum rate of vocalisation occurred in the nights immediately before spawning; this rate receded when larvae were present in the nest, and vocalisations finally stopped after the larvae had dispersed. Vocalisation rate increased again when females restarted to visit the nest site. Long before and also after reproduction, territorial males vocalised with moans and some grunts, when territory intruders evoked escalating agonistic interactions that were correlated with many bites or butts. In agonistic contexts, moan duration, moan peak amplitude frequency and grunt pulse repetition rate differed from the sounds produced during courtship. In *P. marianne,* the generation of sounds during reproductive and agonistic interactions suggests a dual function: attraction of mates and threatening competing males, or potentially egg-eating females.

Key words: Acoustic communication, reproduction, spectral analysis, electric fish, vocalisation, aggression.

*Michael Lamml, Zoological Institute of the University of Regensburg, Universitätsstraße 31, D-93040 Regensburg, Germany. E-mail: michael.lamml@biologie.uni-regensburg.de

INTRODUCTION

Fish detect and respond to sound in various ethologically relevant situations (Myrberg 1981, 1997). Numerous freshwater (for example, Lugli et al. 1995, 1996) and marine fish-species (for example, Myrberg et al. 1993; Lobel & Mann 1995) are active sound producers during reproduction or agonistic interactions (Ladich 1990, 1997, 1998), and a communicative role of acoustic signals has been demonstrated (for example, Myrberg et al. 1986; Ladich et al. 1992; Sparkes et al. 2002; reviewed in Tavolga 1960; Winn 1964; Zelick et al. 1999; Bass & McKibben 2003).

In addition to their characteristic electric sense, which is used in electrolocation and electrocommunication (Lissmann 1958; Bullock & Heiligenberg 1986; reviewed in Kramer 1990, 1996, Moller 1995; Hopkins 1999), mormyrids possess an excellent sense of hearing (von Frisch 1938; Diesselhorst 1938; Kramer et al. 1981; McCormick & Popper 1984; Marvit & Crawford 2000a, 2000b) the anatomical basis of which are highly specialised accessory structures, attached to the sacculus of the inner ear (Heusinger 1826; Stipetić 1939; Yan & Curtsinger 2000; Fletcher & Crawford 2001).

Up to now sound production has been demonstrated in four mormyrid species (reviewed in Crawford 1997). *Gnathonemus petersii* produce single clicks of approximately 25 ms duration during intra- or interspecific agonistic interactions (Rigley & Marshall 1973). "Hoots" are reported for *Petrocephalus ballayi*, during what appears to be agonistic interactions (Crawford 1997). Sound production is well studied in the "strongly acoustic" species *Pollimyrus adspersus* in the laboratory (Crawford et al. 1986; Bratton & Kramer 1989; Crawford et al. 1997b) and, for *Pollimyrus isidori*, in the field (Crawford et al. 1997a). Both sibling species (which substitute each other geographically in their West African range) generate elaborate sounds with species-specific parameters during the reproductive season (Crawford et al. 1997b; Crawford & Huang 1999).

P. adspersus males produce moans, grunts and growls (Crawford et al. 1986; Bratton & Kramer 1989). When the female repeatedly visits the male's territory, males generate long-lasting sequences of moans alternating with grunts (moan-grunt bout). These vocalisations are also evoked by the playback of artificial electric pulse-trains, especially when of the characteristic inter-discharge interval patterns of a female *P. adspersus* which is ready to spawn (Crawford 1991). As courtship advances, males strongly reduce and finally stop sound production altogether before spawning (Bratton & Kramer 1989).

Sound production by territorial male *P. adspersus* and *P. isidori* could play a critical role in mate choice (Crawford et al. 1997b; Crawford et al. 1997a in *P. isidori*). *P. adspersus* have lowest auditory thresholds at frequencies where moans and grunts show highest

energies (Marvit & Crawford 2000b). Intraspecific variability of several moan and grunt characteristics is high; for example, grunt pulse repetition rate and moan spectral peak frequency. Considering their keen hearing, Crawford (1997) and Crawford et al. (1997b) suggest that vocalisations enable *P. adspersus* females to identify individual males and assess their quality.

A fairly common mormyrid in some southern African freshwaters is the dwarf stonebasher *Pollimyrus castelnaui* (Boulenger 1911). It is the smallest living mormyrid and geographically isolated from Central and West African members of its genus. In its southern ranges, the dwarf stonebasher inhabits areas with a markedly seasonal, subtropical climate. Recent studies (Kramer et al. 2003) have demonstrated that the common name dwarf stonebasher comprises an additional, hitherto unrecognised species, *Pollimyrus marianne* Kramer et al. 2003. *P. castelnaui* inhabits the Okavango and the new species *P. marianne* the neighbouring Upper Zambezi system. As suggested by the sophisticated sensory mechanism for detecting minute differences in EOD (Electric Organ Discharge) pulse waveform (Paintner & Kramer 2003), *P. castelnaui* and *P. marianne* might be reproductively isolated not only by geography (which is not absolute because of the intermediate, connecting Kwando system), but also by electroreception (Kramer et al. 2003).

Up to now, nothing was known about the reproductive or acoustic behaviour of *P. marianne*. We found that, similar to *P. adspersus* and *P. isidori*, strong male vocalisations accompany the reproductive behaviours of *P. marianne*. We present a detailed study of their acoustic signalling behaviour in reproductive as well as agonistic contexts, based on infrared video recordings at night.

METHODS

Animals and animal care

Our *Pollimyrus marianne* were caught on 22 August 1999 in a side-channel of the Upper Zambezi River near Kalimbeza/Lisikili, east of Katima Mulilo (17° 32′ 31.9″ S, 24° 26′ 17.7″ E), and transported to our laboratory in Regensburg, Germany. *P. marianne* differs from the Okavango species, *P. castelnaui*, by the distinct waveform of its electric organ discharge and morphological characters, such as the number of scales around the caudal peduncle (SPc; usually 16 versus 12; Kramer et al. 2003). All seven experimental animals were identified as *P. marianne* by their characteristic electric organ discharge waveform.

Three males (male sex determined by an indentation of the anal fin base) and four females were studied in a 600-l aquarium
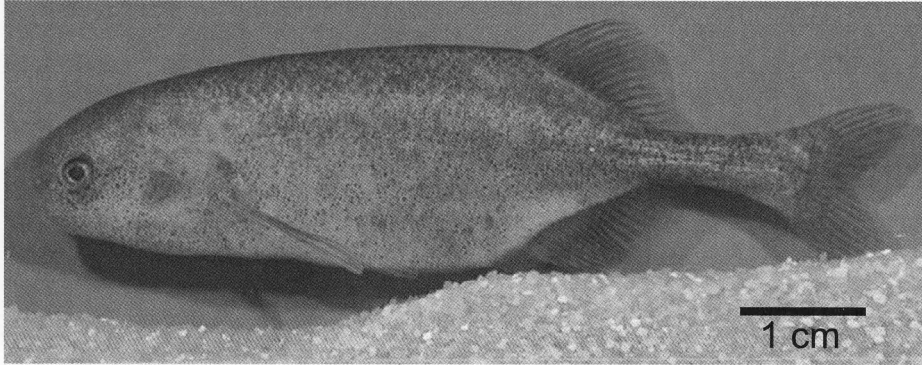
Figure 1. Photograph of *Pollimyrus marianne* male 01 (6.2 cm SL on 10 July 2003) with indented anal fin base.

(240 cm × 50 cm × 50 cm) which was well equipped with stones, roots, ceramic pots and a multi-hole brick as shelters, and densely planted with *Cryptocoryne affinis* and *Vesicularia dubyana*. In June 2004 a single male (male 01, see Figure 1) was transferred into a 780-l aquarium (240 cm × 65 cm × 50 cm) and studied together with two females. In both cases the aquarium bottom was covered by sand (0.3 -1 mm granulation), and an almost noiseless external water filter was used (Eheim model 2213). Water conductivity was held constant within 80-106 µS·cm^{-1}, and temperature within 22.8-28.5 °C over 24 months. The L:D cycle was 12:12 hours. Animals were fed on chironomid larvae (bloodworms) five to six times per week.

Behavioural observations

We collected data on the reproductive behaviour of three male *P. marianne*. In June 2002, February 2003, June 2003 and June 2004, male 01 showed territorial behaviour, built a nest and courted a female. On two of these occasions there were larvae in the nest. Male 01 (6.2 cm SL (Standard Length)) differed from both other males present by body shape, colour, size and individual marks. Male 02 (6.4 cm SL) was distinguished by a slight hump near the posterior head and male 03 (5.5 cm SL) by a black spot on its head. Male 02 showed reproductive behaviour and vocalised in June 2002 and June 2004, and male 03 in June 2004. Number and duration of all behavioural observations are listed in Table 1. We used an observational methodology which can best be described as focal animal sampling by continuous recording (see Martin & Bateson 1987, pages 48-52). We observed the reproductive male (the focal animal) and all interactions occurring with other individuals continuously for at least 30 minutes

TABLE 1

Number of behavioural observations and average number of sounds (± SD) for 30-min recording sessions during different stages of reproductive behaviour in *P. marianne*. ( ) = nights of recording sessions. n.o. = not observed

Male/ reproductive period	30-min observation sessions on no. of nights ( )	Number					
		vocalisations when male predominantly alone in his territory		vocalisations during period of female visits near the nest		vocalisations after period of female visits (male predominantly alone in his territory)	
		Moans	Grunts	Moans	Grunts	Moans	Grunts
Male 01/ June 2002	12 (12)	10.5 ± 14.8	0 ± 0	136.3 ± 21.4	29.0 ± 14.3	15.3 ± 18.6	0.75 ± 0.9
Male 01/ February 2003	30 (13)	n.o.	n.o.	55.8 ± 24.1	37.3 ± 25.2	27.0 ± 6.5	6.0 ± 3.6
Male 01/ June 2003	22 (11)	n.o.	n.o.	47.6 ± 20.1	25.4 ± 15.7	n.o.	n.o.
Male 01/ June 2004	56 (28)	1.0 ± 1.2	0.3 ± 0.8	21.25 ± 13.4	7.8 ± 5.9	5.3 ± 4.5	0.3 ± 0.7
Male 02/ June 2004	20 (10)	1.25 ± 0.9	0.5 ± 1.0	13.1 ± 8.1	14.7 ± 12.9	3.8 ± 0.9	1.16 ± 1.47
Male 03/ June 2004	16 (8)	15.5 ± 0.7	3.5 ± 0.7	26.8 ± 11.5	23.6 ± 6.7	12.1 ± 5.1	3.4 ± 2.9

TABLE 2

Summary of estimated sound characteristics and how they were determined

Sound type	Sound characteristic	Description of sound characteristic	Used data source and measuring methodology	Illustrated in Figure	Values in Table
Moan	Moan duration	Time from onset to end of sound.	Sonogram after resampling the vocalisation at 24 kHz (temporal resolution, 2.6 ms).	3 A, B	3, 4
	Moan peak-amplitude frequency	Average frequency at peak amplitude of the amplitude spectrum.	Amplitude spectrum. Whole sound or, when the moan was longer than 2 s, a section of 2 s duration where H2 showed lowest frequency modulation (frequency resolution, 0.366-0.732 Hz).	3 C	3, 4
	Frequency of moan higher harmonics	Average frequency of the higher harmonics in the amplitude spectrum.	Amplitude spectrum. Whole sound or, when the moan was longer than 2 s, a section of 2 s duration where higher harmonics showed lowest frequency modulation (frequency resolution, 0.366-0.732 Hz).	3 C	4
	Moan H2min	Minimum frequency of the moan second harmonic.	Sonogram. Minimum of H2 in the sonogram of the whole sound after resampling at 6 kHz (frequency resolution, 5 Hz).	3 B	4
	Moan H2max	Maximum frequency of the moan second harmonic.	Sonogram. Maximum of H2 in the sonogram of the whole sound after resampling at 6 kHz (frequency resolution, 5 Hz).	3 B	4
Grunt	Moan-grunt bout duration	Time from onset to end of moan-grunt bout.	Sonogram after resampling the vocalisation at 24 kHz (temporal resolution, 2.6 ms).	5	3, 4
	Grunt period	Time interval between the onset of consecutive grunts.	Oscillogram (temporal resolution, 40 µs).	4 A	3, 4

Grunt duration	Time from peak of the first grunt pulse to peak of the last grunt pulse.	Oscillogram (temporal resolution, 40 µs).	4 B	3, 4
Pulse number	Number of pulses per grunt.	Cursor function of the zoomed oscillogram.	4 B	3, 4
Grunt pulse duration	Time from onset to end of one grunt pulse.	Cursor function of the zoomed oscillogram (temporal resolution, 40 µs).	4 B"	3, 4
Grunt inter-pulse interval (IPI)	Time interval between the consecutive peaks of grunt pulses.	Grunt duration divided by the number of intervals (= n grunt pulses - 1) (see Crawford et al. 1997b).	4 B'	3, 4
Grunt pulse repetition rate (PRR)	Number of grunt pulses per second.	Reciprocal of the inter-pulse interval.	4 B	3, 4
Grunt frequency of H2	Average frequency of the second harmonic of the amplitude spectrum.	Amplitude spectrum. Whole grunt (frequency resolution, 0.732-2.93 Hz).	4 D	4
Grunt peak-amplitude frequency	Average frequency at the peak amplitude of the amplitude spectrum.	Amplitude spectrum. Whole grunt (frequency resolution, 0.732-2.93 Hz).	4 D	3, 4

per night from the onset of dark. On 7-8 February 2003 (during 24 hours) we observed male 01 continuously for 4 hours after onset of dark and for one hour before daylight. During the remaining hours of the 24h observational session we observed this male during 10 minute sampling intervals at the beginning of every hour.

Fish behaviour was videotaped using infrared illumination and an infrared-sensitive camera (model: Pieper FK 6990-IQ, videotape recorder: Panasonic AG-7330, Hifi, S-VHS). A single-cycle sine-wave pulse of 2 ms duration, recorded on audio track no. 1, triggered a pulse marker at 4-s intervals which generated a synchronisation signal on the video image. This allowed for synchronisation of motor behaviour and vocalisations (see below) at a resolution of better than ± 40 ms.

Analysis of acoustic signals

We monitored acoustic signals of the three reproductive *P. marianne* males with a hydrophone (Brüel & Kjær Model 8101, 1 Hz - 125 kHz frequency response), positioned in the territories of the males near their nest at an approximately 10cm distance. Sounds were amplified with a measuring amplifier (Brüel & Kjær Model 2610, 2 Hz – 200 kHz frequency response) and tape-recorded on the second audio-track of the video recorder. Moans and grunts were assigned to the males by the temporal correlation between relative sound pressure level and fish distance from the hydrophone. However, when two fish were interacting too closely (for example, circling during agonistic interactions; Figure 7), it was not possible to assign vocalisations to a specific individual based on relative sound pressure level. For estimating rates of vocalisation during reproductive behaviours, a new vocalisation was tallied after a period of silence of one second.

For sound analysis the vocalisations with the best signal-to-noise ratio, typically generated within 5-20 cm of the hydrophone, were digitised at 48 kHz sampling rate and 16 bit vertical resolution using the standard soundcard of an IBM - compatible computer (Pentium IV, 1.7 GHz), controlled by the software Avisoft-SASLabPro Version 4.23b (Avisoft Bioacoustics, Berlin, Germany). To reduce low-frequency noise, the amplified hydrophone output was bandpass-filtered (40 Hz to 10 kHz pass-band) using an electronic filter (Wavetek-Rockland Model 452; linear phase response). All sounds used for analysis of sound characteristics were recorded with this filter setting.

Table 2 summarises all sound characteristics, specifies the used data sources and describes the measuring methodology. Temporal parameters, such as grunt duration, pulse duration and inter-pulse intervals (with the exception of moan duration and moan-grunt bout duration), were measured from sound pressure oscillograms at an
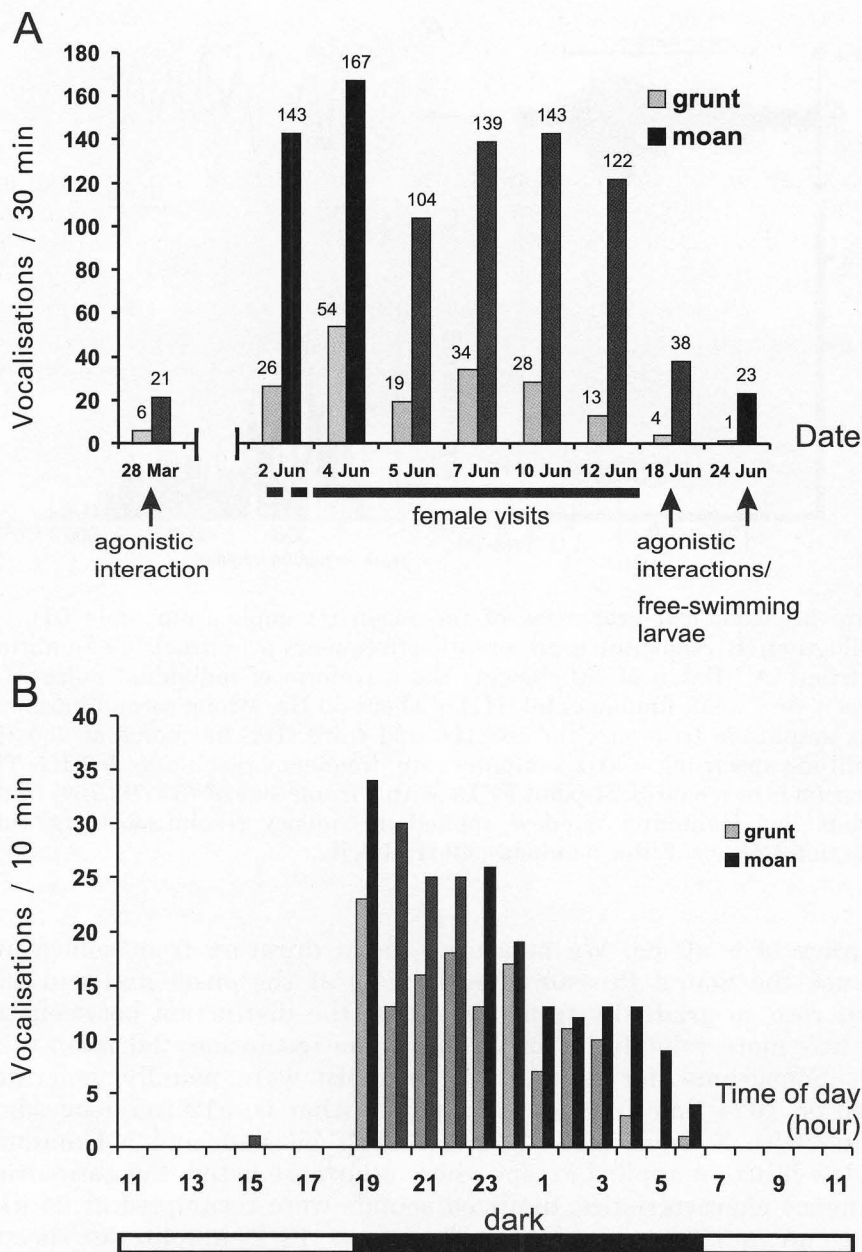
Figure 2. (A) Moan and grunt rates before and after the onset of male 01's reproductive activity (before, 28 March 2002; after, June 2002). (B) Rate of vocalisations over 24 hours on 7-8 February 2003. Vocalisations were almost exclusively produced during the nocturnal activity phase. Vocalisations began immediately with the onset of dark and continuously decreased in number during the night.
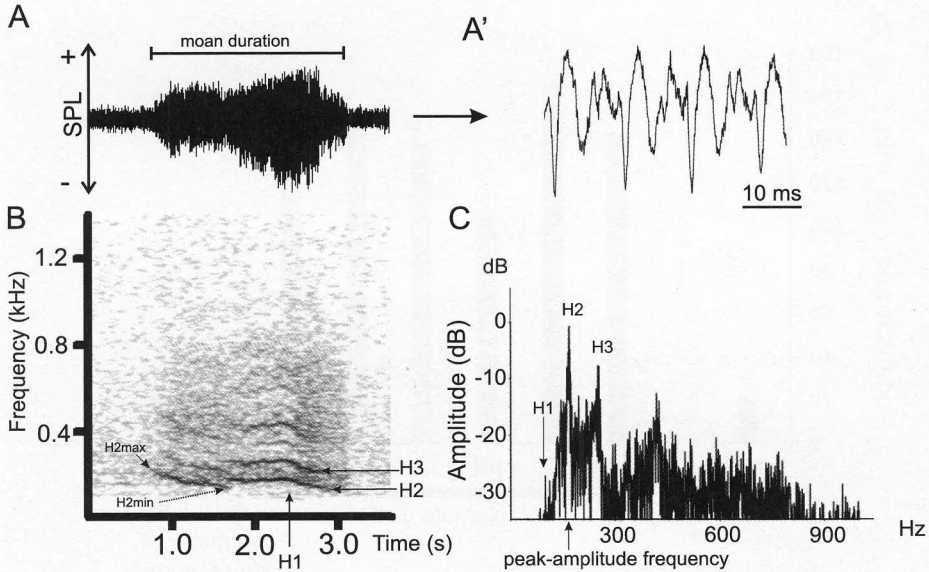
Figure 3. Acoustical properties of the moan (example from male 01). (A) Oscillogram, (B) Sonogram representation (frequency over time). (C) Amplitude spectrum. (A´) Detail of (A) showing the waveform of individual pulses. (B) shows a very weak fundamental (H1) of about 80 Hz, strong second harmonic [peak-amplitude frequency] at 168 Hz, and third (H3) harmonic at 250 Hz. Amplitude spectrum: 5 kHz sampling rate, frequency resolution: 0.3 Hz. The sonogram is based on 1024-point FFTs, with a frame size of 75%, 93.75% frame overlap, and Hamming Window applied. Frequency resolution 4 Hz, time resolution 12.8 ms. Filter bandpass, 40 Hz-10kHz.

accuracy of ± 40 µs. We measured moan duration from sonograms because the Sound Pressure Level (SPL) at the onset and end of a moan rose so gradually from noise that the distinction between the two was more reliable in sonograms (time resolution: 2.6 ms).

Sonograms (for example, Figure 3B) were usually generated based on 1024 time function data points (that is, 512 frequency data points) with a frame size of 75%, 93.75% overlap, and a Hamming window function applied except where otherwise noted. For estimating frequency characteristics, digitised sounds were resampled at 24 kHz using an anti-aliasing filter. Therefore, FFT amplitude spectra comprised between 4096 to 32 768 frequency data points (resolution: 0.366-2.9 Hz). The signal-to-noise ratio was about -30 dB as determined from test sounds generated at identical conditions by an underwater loudspeaker, model UW-30 Diatran (University Sound, Oklahoma City), driven by a sine wave generator (Hewlett-Packard Model 3314A) at 500 Hz via a power amplifier (Model AD5250B; Sherwood Europe GmbH). The amplitude of the test sounds generated was adjusted to
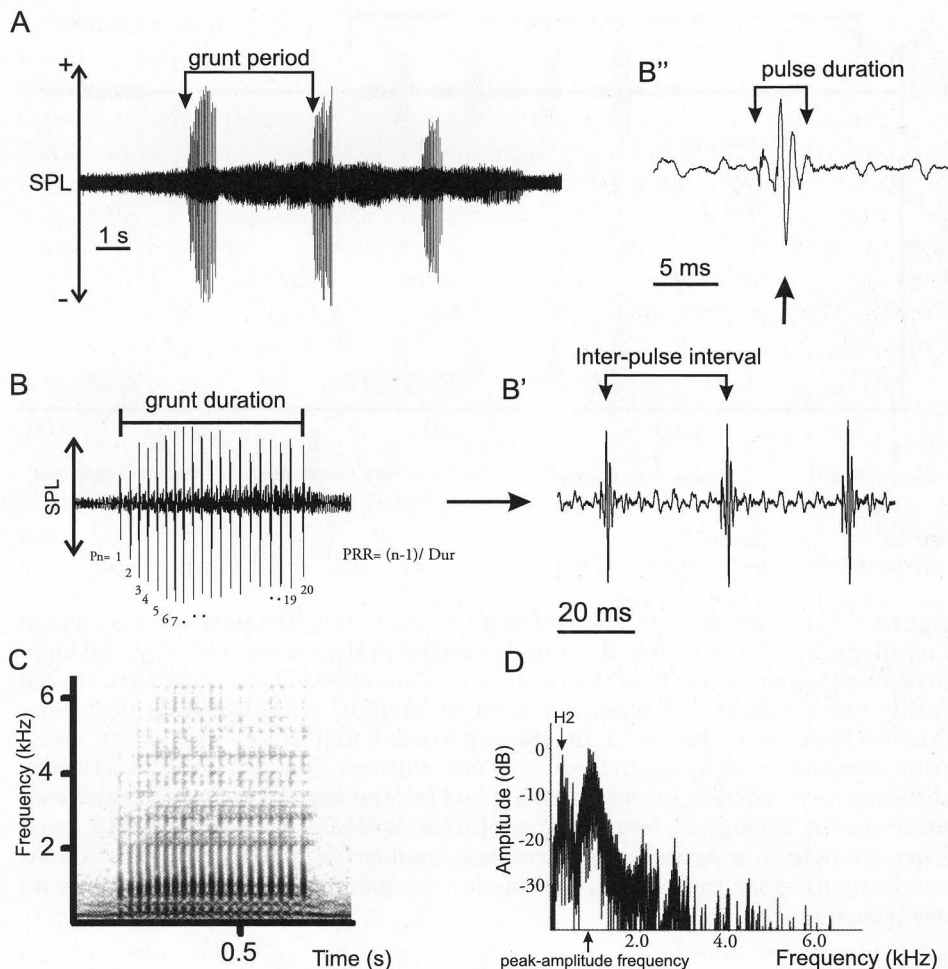
Figure 4. Temporal and spectral parameters of a moan-grunt bout at increasingly higher resolution. (A-B´´) Ordinate, SPL; abscissa, time. Grunt period, grunt inter-pulse interval, pulse duration, as indicated in graphs. (B´) Detail of the waveform in (B) at high temporal resolution. Acoustic pulses are repeated at fairly regular intervals which resulted in a regular pulse period. The oscillations between pulses probably represent the superimposed moan. (C-D) Spectral properties of the grunt (with superimposed moan of weaker amplitude). (C) Sonogram for grunt in (B), at same time scale. (D) Amplitude spectrum for the whole grunt in C. During the grunt the moan harmonics were shifted towards higher frequencies (H2 at about 200 Hz in male 01) because of frequency modulation. The grunt peak-amplitude frequency (of 845 Hz) is not harmonically related to the oscillations of the superimposed moan. Amplitude spectrum: 8192 frequency data points (HF region not shown), frequency resolution, 1.46 Hz. The sonogram is based on 1024-point FFTs, 50% frame size, 93.75% frame overlap, and Hamming Window applied. Frequency resolution, 23 Hz; temporal resolution, 2.6 ms.
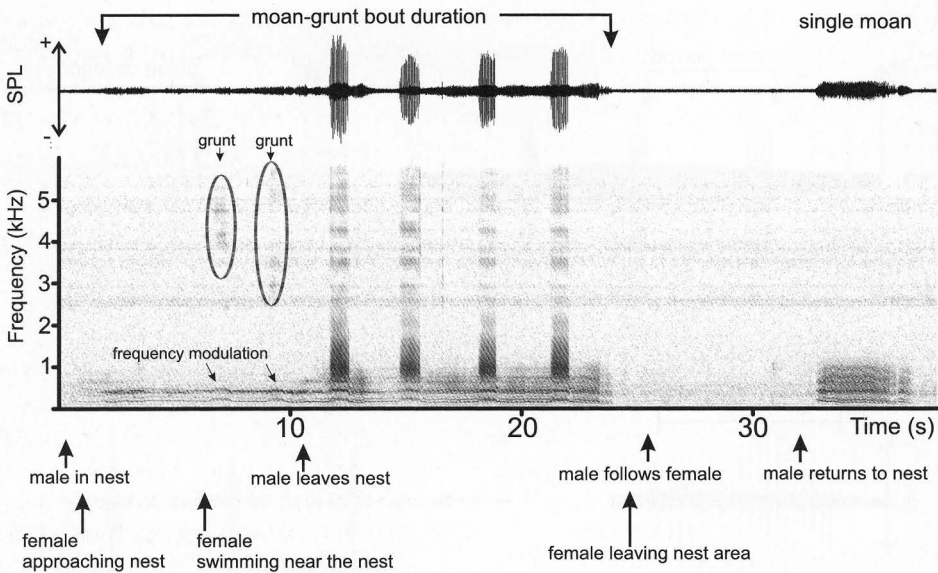
Figure 5. Moan-grunt bout when a female visited male 01's nest site (sonogram + oscillogram). Shortly after the female arrived in the male's territory, the male gave a long moan-grunt bout (6 grunts per 17 seconds). The first two grunts are hardly noticeable on the sonogram because male 01 was still in its nest hole, shielded from the hydrophone. In addition to weak high-frequency energy, these grunts are indicated by moan frequency modulations. During this interaction no butts or bites occurred. After the female had left the male's territory, it produced a pure moan. Sonogram frequency resolution, 23 Hz; time resolution, 10.7 ms. Even though this sound sequence was inadvertently filtered with an A-weighting network that attenuated the low-frequency range, it is shown for its ethological relevance.

that of an average moan, as recorded on the hydrophone measuring-amplifier (104 dB re: 1 µPa at about 10 cm distance). For estimating the degree of frequency modulation within a moan we measured minimum and maximum frequency of the second harmonic of the moan (H2min, H2max), using the cursor function of the sonogram representation in Avisoft after resampling the vocalisation at 6 kHz. Two sound sequences (shown in Figures 5 and 7) had inadvertently been recorded with the "A weighting network" of the B&K measuring amplifier switched on. Therefore, in these two sonograms frequencies below 900 Hz appear weaker than they are in reality. The recordings in Figures 5 and 7 were excluded from all amplitude-related data analysis, and are solely shown for their ethological relevance regarding the concomitant motor behaviour.
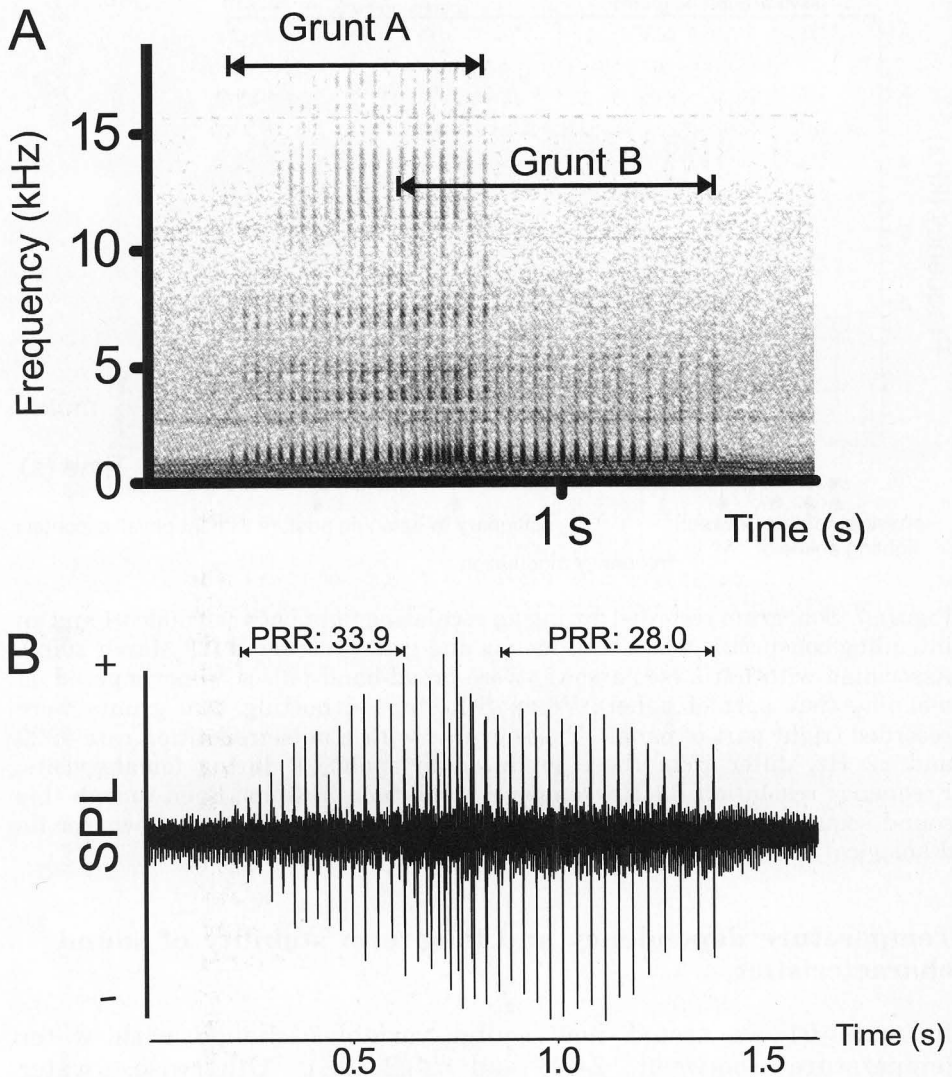
Figure 6. Two superimposed grunts generated by male 01 and male 02. (A) sonogram. Amplitude spectra from non-overlapping sections of the grunt recordings were individually different: for example, peak-amplitude frequency of Grunt A differed from Grunt B (1042 Hz rather than 968 Hz, respectively). A second peak (at 3512 Hz) was lacking in Grunt B. (B) oscillogram with same time scale as (A). PRR of Grunt A was 33.9 in contrast to 28 in Grunt B. The sonogram is based on 1024-point FFTs, 75% frame size, 87.5% frame overlap, and Hamming Window applied. Frequency resolution, 23 Hz; temporal resolution, 2.6 ms.
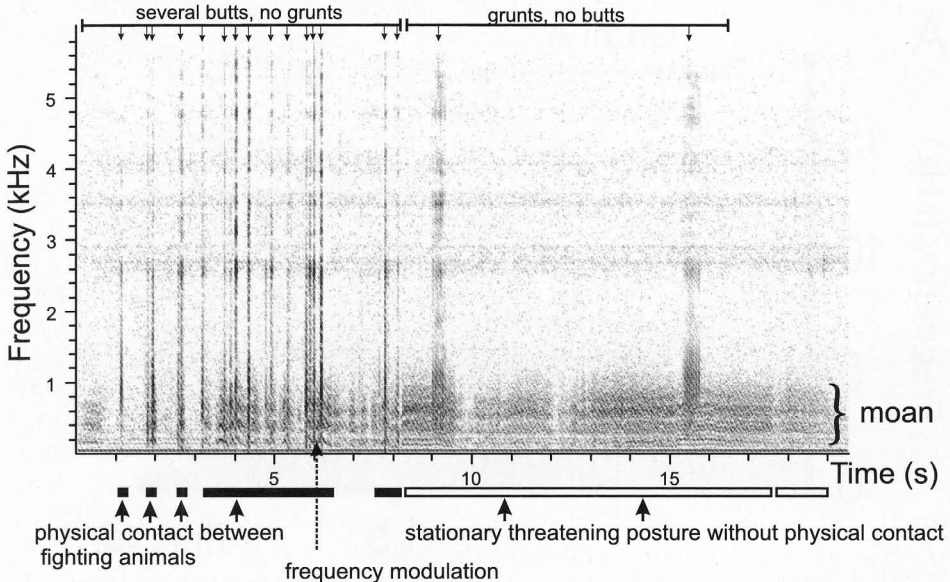
Figure 7. Sonogram recorded during an escalating fight between male 01 and an intruding conspecific when both moans and grunts occurred (28 March 2002). Associated with butts (see arrows) were broad-band pulses, superimposed on moaning (left part of panel). When fish stopped butting, two grunts were recorded (right part of panel). These grunts with a pulse repetition rate of 20 and 22 Hz, differ from those produced by male 01 during female visits. Frequency resolution, 11 Hz; temporal resolution, 21.3 ms. Even though this sound sequence was filtered with an A-weighting network it is shown for its ethological relevance.

Temperature dependency and long-term stability of sound characteristics

In male 01 we tested how sound variables change with water temperature (between 24.7 and 28.2 °C). Otherwise, water temperature (± 0.1 °C) remained stable at 25.5 ± SD 0.2 °C. Vocalisations were recorded from the onset of dark (7.00 p.m). We calculated Q_{10} values using the van't Hoff equation: $Q_{10} = (R_2/R_1)^{(10/T2 - T1)}$ (see, for example, Schmidt-Nielsen 1997).

We determined standard length (SL) of male 01, defined as the distance between tip of snout and base of tail-fin with an accuracy of ± 1 mm, before, during and after the observational period from photographs taken on 13 February 2002, 10 July 2003 and 1 July 2004.

Statistical analysis was performed using the software Prism V. 3.00 (GraphPad). Temperature dependency of sound characteristics was tested by linear regression analysis, whereas the long term stability of sound characteristics and differences in sound

characteristics during agonistic and reproductive behaviours were tested with an unpaired Student's t-test. We chose a *P*-value of = 0.05 (two-tailed) as the significance level when to reject H_0.

RESULTS

Reproductive behaviour

The first indication of a male *P. marianne's* reproductive behaviour was an increase in territorial behaviour, and the presence of a nest built from plant material (Java moss, *Vesicularia dubyana)* in a dark space (hole in a brick, or under a root), observed in all three male *P. marianne.* The other specimens of *P. marianne* present were resting individually in various shelters during daytime, but gathered after dark and together searched for food in all parts of the aquarium. The territorial males did not join this group but remained within about 25 cm of their nest, and aggressively chased away any other fish. Initially they attacked females as well as males approaching the nest.

This was also the time when the first vocalisations occurred (see Table 1, Figure 2). Males produced two distinct sounds, one tonal and harmonically structured (the moan, Figure 3), the other consisting of a regular sequence of broadband pulses (the grunt, Figure 4). The terms moan and grunt were adopted from Crawford et al. (1986) who had described similar sounds for *P. adspersus.* Immediately after dark the males started vocalising (Figure 2B). As long as the males remained in their territory alone, the males produced only moans, or, when a certain female passed the male's territory, moans with a single grunt.

In the next stage of the reproductive cycle the female's initially brief visits became longer and closer to the nest site with reduced or even no aggression from the male. When females started visiting the males' territories (for example, male 01 on 4 June 2002 at night) males began vocalising moan-grunt bouts (that is, one single grunt or a series of grunts superimposed on a long moan; Figure 5). Initially, females were attacked in the male's territory but tolerated later on. The rate of vocalisation increased considerably with the frequency and duration of female visits to the males' territories. This stage of frequent female visits lasted one or even several days when long-lasting moan-grunt bouts were given at the highest rate (Table 1).

Figure 5 shows as sonograms an episode of sounds generated during a female's visit. Even before the female arrived in his territory, male 01 had produced a single moan while hovering in the hole of the brick that held his nest. When the female was within 5 cm of the nest the male approached the female and produced a long-lasting moan-grunt bout (6 grunts per 17 s). The male did not show any aggressive

behaviour towards the female during this interaction (minimum distance between male and female approx. 3 cm). After the female had left the territory, the male produced again a single moan.

Unfortunately, we were unable to observe spawning behaviour directly, although females continued visiting the males' territories. However, the presence of eggs or larvae in the nests of the three males were clear testimony for successful spawning in four of six observation periods. When the first free-swimming larvae were seen in the vicinity of the nest, the rate of vocalisations decreased (for example, male 01, 18 June 2002), and finally stopped completely when the reproductive period was over (male 01, 0 moans, 0 grunts per 30 min recorded on 19 November 2002). Nevertheless, even in the presence of free-swimming larvae, males 02 and 03 increased their rate of vocalisation again when females started to visit the males' territories again, indicating a renewed readiness for reproduction (June 2004).

In June 2002 grunts of a second male 02 occurred simultaneously with the vocalisations of male 01. These grunts overlapped or alternated with moan-grunt bouts of male 01 and had a very low sound pressure level (because male 02 was usually farther away from the hydrophone than male 01). Figure 6 shows two overlapping grunts of almost the same amplitude, produced by both males simultaneously.

Description of sounds

All three males produced two different types of sounds, long-lasting tonal moans and short pulsatile grunts (see Table 3 and 4).

Moan. The moan (Figure 3) is a tonal sound of highly variable duration (mean: 2.26 ± SD 0.6 s), composed of a stereotyped group of acoustic pulses that were repeated hundreds of times per moan. The spectral property of the moan is "noisy harmonic" (as shown in Beeman 1998, p. 75) with a weak fundamental (H1, only seen in moans with a very high SPL) at about 80 Hz that was only slightly frequency-modulated, and higher harmonics at 166 ± SD 9.3 Hz (H2, mean peak-amplitude frequency) and at about 241 Hz (H3) in male 01, with similar values for male 02 (151 ± SD 8.0 Hz, H2, and about 211 Hz, H3). Never was the first harmonic (H1) the strongest in all males. Single moans were sporadically generated during the night while the males remained in their territory, with no detectable social interaction. Most of these moans occurred when the males were slowly swimming through their nesting area or hovered near the nest.

Grunt. Especially during female visits we observed a second vocalisation, the grunt, which differed from the moan in (i) the higher sound pressure level, (ii) the greater spectral bandwidth, and (iii) a marked spectral peak at a mean 1019 Hz (Figure 4; Table 3 and 4).The

TABLE 3

Comparison of sound characteristics for vocalisations of male *P. marianne* (mean plus range), *P. adspersus* and *P. isidori* (means ± SD). Sound variables for three *P. marianne* males (at least 8 moan-grunt bouts and 15 sounds per fish and temperature) as estimated during reproductive behaviour (June 2004). *P. adspersus* and *P. isidori* data from Crawford et al. 1997b (water temperature: 28 °C), *P. adspersus*, n= 15 males. *P. isidori* data: 27 recording sessions at 7 distinct locations in the field. *n* = Number of individuals

	P. marianne (n= 3)				*P. adspersus*	*P. isidori*
Water temperature	25.4 ± 0.15 °C		27.7 ± 0.4 °C		n= 15 males	
Moan duration (ms)	2260	(1600-2800)	1897	(1520-2151)	812 ± 495	121 ± 35
Moan peak-amplitude frequency (Hz)	165	(151-180)	175	(160-184)	240 ± 12	332 ± 34
Moan-grunt bout duration (s)	14.69	(12.57-17.10)				
Grunt period (s)	3.15	(3.0-3.26)				
Grunt duration (ms)	596.5	(563-618)	561	(422-638)	229 ± 86	268 ± 94
# Pulses per grunt	18.1	(17-20)				
Grunt pulse duration (ms)	3.4	(3.2-3.7)				
Grunt inter-pulse interval (ms)	31.2	(30.2-32.6)				
Grunt pulse repetition rate (Hz)	32.1	(30.7-33.1)	35.8	(34.7-37.2)	56 ± 3	44 ± 4
Grunt peak-amplitude frequency (Hz)	1019	(888-1116)	1076	(872-1180)		

TABLE 4

Moan and grunt characteristics of vocalising *P. marianne* males. *) Median and SIQ (= semi-interquartiles) for count measures.
All sounds were passband-filtered at 40 Hz-10 kHz. (n = number of observations). Water temperature, 25.4 ± 0.15 °C (June 2004)

	Moan					Grunt								
	Moan dura-tion	Fre-quency of peak amplitude	H2 min	H2 max	H3	M-G bout duration	Grunt period	Grunt duration	#Pulses per grunt	Pulse duration	Inter-pulse interval	Pulse repeti-tion rate	Fre-quency of H2	Fre-quency of peak
	(s)	(Hz)	(Hz)	(Hz)	(Hz)	(s)	(s)	(ms)		(ms)	(ms)	(Hz)	(Hz)	(Hz)
Male 01														
Mean/ Median *)	2.8	166	120	193	241	14.4	3.0	563.4	17*)	3.7	30.8	32.5	216	888
Minimum	1.6	139.8	99	169	207	5.9	1.65	220	8	3.5	26.5	28.86	177	688
Maximum	6.2	180	146	216	258.5	31.8	6.89	1020	30	3.99	34.6	37.73	280	1062
SD/ SIQ *)	1.03	9.3	12.4	10.6	13.6	7.7	1.09	144.7	5.5*)	0.111	1.58	1.69	24.3	85
n	23	23	23	23	23	10	36	46	46	457	46	46	45	45
Male 02														
Mean/ Median *)	2.38	151	120	170	211	12.57	3.26	618.2	20*)	3.29	30.2	33.1	205	1054
Minimum	1.19	139	105	158	187	7.64	1.43	388	13	3.1	28.3	30.12	180	915
Maximum	4.0	162	134	205	228	25.45	7.88	888	29	3.5	33.2	35.34	230	1203
SD/ SIQ *)	0.97	8.0	7.7	13.1	13.2	5.57	1.46	126.9	3.8*)	0.12	1.37	1.46	13.1	90
n	15	15	15	15	8	8	25	16	16	160	16	16	16	16
Male 03														
Mean/ Median *)	1.6	180	145	209		17.1	3.2	608	17.5*)	3.28	32.6	30.7	192	1116
Minimum	0.74	162	117	175		6.9	1.39	382	13	3.03	28.3	27.5	170	1006
Maximum	2.9	195	169	269		33.2	9.7	1029	31	3.4	36.4	35.2	215	1224
SD/ SIQ *)	0.65	8.7	15	23.2		7.8	1.5	159.9	4.6*)	0.11	2.4	2.39	12.0	59
n	15	15	15	15		9	39	16	16	160	16	16	16	16

TABLE 5

Least-squares linear regression of the dependency of moan and grunt characteristics on water temperature in *P. marianne* male 01.

Dependent variables	Q_{10}	linear regression							Nonlinear?
	(24.7-28.2 °C)	Slope	y intercept	r^2	F ratio	df_n	df_d	P	P (runs test)
Moan duration	1.06	-0.0686	3.918	0.0099	0.5500	1	55	0.4615	0.9000
Moan peak-amplitude frequency	1.80	8.224	-47.30	0.3358	27.81	1	55	<0.0001	0.5000
Grunt duration	1.99	-0.03689	1.465	0.1105	6.955	1	56	0.0108	1.0000
Grunt peak-amplitude frequency	0.92	-4.163	1001	0.00275	0.1742	1	63	0.6779	0.5000
Grunt pulse repetition rate	2.02	2.042	-20.67	0.6054	105.9	1	69	<0.0001	0.9000

grunt is a short pulsatile vocalisation of 596 ms mean duration, composed of acoustic pulses that are spaced at regular intervals of about 31 ms. Grunts superimposed an ongoing moan, forming a "moan-grunt bout". Therefore, at high temporal resolution, we saw not only series of single grunt pulses but also additional oscillations, probably representing the moan (Figure 4B').

The moans generated by the three males of the present study were similar but differed quantitatively in several variables (Table 4). In agreement with their size, the largest fish generated moans of the lowest peak-amplitude frequency (151 Hz), and the smallest of the highest (180 Hz). The peak amplitude frequency represented the H2 of a moan, as shown by the presence of an H1 of half that frequency (that was very weak but distinct in good recordings from all three fish), and an H3 component of three times the respective H1 frequency. Still higher harmonics, H4 and H5, were also seen in some recordings. The Grunt PRR ranged from 30.7 Hz in the smallest (male 03) to 33.1 Hz in the largest fish (male 02).

Temperature dependency of male 01's sound characteristics

Most sound characteristics depended on water temperature (Table 5). All least-squares regression lines (not shown) are linear (nonlinearity, non-significant; $P = 0.5$, runs test). Moan peak-amplitude frequency increased with water temperature ($Q_{10} = 1.8$), but grunt peak-amplitude frequency ($Q_{10} = 0.92$) seemed to be temperature-independent, perhaps because of the technical difficulty of determining a broadly rounded peak. Moan duration did not change significantly; however, grunt duration decreased with water temperature. Therefore, we calculated the Q_{10} based on the reciprocal of moan and grunt duration, resulting in Q_{10} values of 1.06 for moan duration and 1.99 for grunt duration. However, temperature explains only 0.9 % of the variation in moan duration and 11 % in grunt duration. Grunt PRR increased with temperature following a Q_{10} of again close to 2.

Long term variability of male 01's sound characteristics

The standard length of male 01 (6.2 cm) did not change within the observational period (13 Feb 2002 - 10 Jul 2004). At an age of at least 3 years at the beginning of the observations, male 01 was obviously fully-grown and remained in very good health during this period. For the whole observational period, moan duration had not changed for male 01 whereas moan peak-amplitude frequency increased significantly (from 154 Hz to 166 Hz; Table 6). Grunt duration

TABLE 6

Long-term stability of moan and grunt characteristics in *P. marianne* male 01.
P values in bold type, < 0.05 (two-tailed)
n = no. of observations

Variable	June 2002			June 2004			
	Mean	SD	*n*	Mean	SD	*n*	*P*
Moan duration (s)	2.58	1.39	106	2.81	1.03	23	0.4697
Moan peak-amplitude frequency (Hz)	154.2	13.3	104	166.6	9.3	23	**< 0.0001**
Grunt duration (ms)	573.39	195.7	57	563	144	46	0.7747
Grunt peak-amplitude frequency (Hz)	922	103.4	57	888	85	45	0.0801
Grunt pulse repetition rate (Hz)	31.52	23	57	32.5	1.69	46	**0.0171**

shortened (not significantly) from 573 ms to 563 ms, and grunt peak-amplitude frequency also remained nearly constant between 922 Hz and 888 Hz (difference ns); but grunt PRR increased significantly from 31.5 to 32.5 Hz.

Sound production during agonistic interactions

Males defended their territory and nest site from the beginning of reproductive behaviour (for example, male 01, 28 March 2002) to the time when the free-swimming larvae left the nest (for example male 01, 18 June 2002). Normally, a short attack was sufficient to chase away intruding conspecifics. However, sometimes an intruder did not retreat and interactions escalated into fights that were accompanied by moans and grunts. Agonistic interactions with concurrent sound production were observed in male 01 (9 moans, 2 grunts during 3 agonistic interactions) and male 03 (16 moans, 0 grunts during 7 agonistic interactions) but not in male 02.

Figure 7 shows a sonogram of the sounds produced during a fight on 28 March 2002. Both fish circled round one another very quickly, mutually directing many bites or butts (> 15) at the frontal head and back of the opponent (resulting in as many broad-band pulses in the sonogram). The only vocalisations during the circling were moans, with very short (approx. 100 ms) modulations of the peak-amplitude frequency of about 80-100 Hz. During the subsequent, stationary threatening display, two grunts (PRR, 20 and 22 Hz) were produced in addition to an ongoing moan. The PRR of these two grunts were much lower than the PRR of grunts recorded during female visits (minimum observed in male 03: 27.5 Hz). The ongoing moan was similar in H2 (136 Hz) and H3 (200 Hz) to male 01's moans generated during reproductive behaviours in June 2002, but could have also been produced by male 02 which showed an overlapping distribution of moan spectral characteristics.

Moans given during agonistic circling were significantly shorter than moans displayed during reproductive behaviours in male 01 (moan duration: 0.63 ± SD 0.68 s, n= 9, Student's t-test, $P<$ 0.0001, and male 03, and also higher in this male's moan peak-amplitude frequency (moan duration: 0.57 ± SD 0.49 s, n= 16, Student's t-test, $P<$ 0.0001; moan peak-amplitude frequency: 213 ± SD 31 Hz, n= 16, Student's t-test, $P < 0.0005$). Based on the characteristic spectral frequency distribution of the moans (average moan H4 during agonistic interactions, 451 Hz) we believe they were from male 03. After the fights both males still occupied their territories and continued their reproductive behaviours (nest-building and protecting the nest site until the larvae dispersed). Therefore, we believe that the fighting did not affect the hierarchy within the aquarium, or else, the owner of the territory was also the dominant individual.

DISCUSSION

Reproductive behaviour

Up to now, next to nothing was known about the behaviour, especially reproductive behaviour, of the dwarf stonebasher from the Upper Zambezi system (nor *P. castelnaui* from the Okavango; Skelton 2001, Kramer et al. 2003). The dwarf stonebasher inhabits the dense vegetation of river banks and lagoons, shallow streams, and also rock crevices. In the Upper Zambezi, *P. marianne* were found not only in the bottom region but also in the water column in dense vegetation of grass, reed and papyrus, as well as at the surface under the floating leaves of water-lilies during daytime (B.K. pers. obs.).

Similar to *P. adspersus* (Kirschbaum 1987) and *P. isidori* (Crawford et al. 1997a), in *P. marianne* a nest made of filamentous plant material, placed in a narrow, dark space (such as a hole in a brick, or under a root), held the eggs. Microzooplankton present in the aquarium probably served the larvae for food (Høberg et al. 2002). The males established a territory (approx. 50 cm diameter) and defended it against conspecifics of both sexes. The territory size is likely to be affected by the limited space within an aquarium. During the main reproductive phase, females visited the territory and nest area, a behaviour typical also for female *P. adspersus*. Like in *P. adspersus,* the male defended developing eggs and larvae. *P. marianne* male 01's reproductive period in the laboratory, beginning with territory establishment and ending with free-swimming larvae, lasted about 3 months. We believe there were several spawning cycles within this period. The hypothesis of fractional spawning during several short cycles is strengthened by observations on males 02 and 03 whose rates of vocalisation increased when females started to visit the nest site again, even when larvae were still present.

Thus we confirm similar reproductive behaviour, territory establishment, nest-building and parental care for the eggs and young by the male parent, as observed in two other members of the genus *Pollimyrus* (Kirschbaum 1987; Bratton & Kramer 1989; Crawford et al. 1997a; Kirschbaum & Schugardt 2002).

Sound production

The present study clearly demonstrates sound production during reproductive behaviours in three male *P. marianne,* with acoustic features similar to, but also clearly different from, those observed in *P. adspersus* and *P. isidori* (Crawford et al. 1986, 1997a, 1997b). Similar to these species, during *P. marianne's* reproductive cycle the rate of sound production increased, reaching a peak during presumed spawning nights. When the larvae had absorbed all their yolk and

begun to range freely, their father's sound production decreased and finally stopped completely (male 01 in June 2002), or increased again when females showed renewed interest for the male's nest site (males 02 and 03 in June 2004).

As in *P. isidori,* the vocal repertoire consisted of two distinct sounds, a tonal moan and a harsh grunt. However, *P. marianne* differed greatly from *P. adspersus* and *P. isidori* in the typical sequence of sound patterns. Whereas *P. adspersus* produced moans alternating with grunts, sometimes followed by growls, in *P. isidori* a grunt was followed by several moans (Crawford et al. 1997b). Three male *P. marianne,* however, either produced moans (without grunts), a moan superimposed by a single grunt, or, when females visited the males' territories, a long-lasting moan that was superimposed by several grunts. Growls (as observed in *P. adspersus*) were never observed in *P. marianne*. Moreover, some acoustic characteristics of *P. marianne* vocalisations differed quantitatively from those of both other *Pollimyrus* species (see Table 3). At almost the same water temperature (27.7 °C), *P. marianne* moans were much longer than those of *P. adspersus* and *P. isidori,* and grunts lasted nearly twice as long at a pulse repetition rate that was much lower than in both other species.

During long moan-grunt bouts, grunts superimposed an ongoing moan. This might result from two fish vocalising simultaneously. However, the relative sound pressure level of the grunt and the moan changed in concert with the distance between a certain vocalising male from the hydrophone. Therefore, we believe that in these instances one individual male generated moans and grunts simultaneously, suggesting two independent sound producing mechanisms. However, because during a grunt a moan was frequency-modulated (for example, in male 01 the H2 was shifted upwards to about 200 Hz), the two sound-producing mechanisms do not seem to be totally independent of each other.

At constant standard length, sound characteristics of male 01 varied only slightly over two years of observation, but depended greatly on water temperature. Q_{10} values for moan peak-amplitude frequency, grunt duration and grunt PRR were close to 2 and similar to those reported for *P. adspersus* (Crawford et al. 1997b). The grunt peak-amplitude frequency did not change significantly with water temperature. The moan peak-amplitude frequency was affected by temperature, probably because it is determined by the frequency of sonic muscle contractions whereas grunt peak-amplitude frequency might depend mainly on the resonance properties of the swimbladder and hence be independent of temperature. The grunt PRR was affected by temperature probably because it is also dependent on the sonic muscle contraction rate.

For *P. adspersus*, important functions of vocalisations in mate choice and localisation are discussed by Crawford (1997) and Crawford et al. (1997b). This species' range of highest auditory sensitivity (200-900 Hz) matched the frequency range where moans and grunts showed highest energy levels; lowest just noticeable differences (jnd) were found in this range (8.5 ± SE 1.9 Hz at 500 Hz; Marvit & Crawford 2000b). *P. adspersus* is also capable of discriminating minute differences in the repetition rate of brief artificial acoustic clicks (CRR, see Marvit & Crawford 2000b) with jnds of 300 μs in the 10 to 15 ms inter-click interval range (an approx. 3% difference). Similar jnds were demonstrated for electrical pulse trains of 20 Hz: trained *P. adspersus* detected a 2% change (Kramer & Heinrich 1990). The sounds generated by the three males of the present study differed distinctly amongst each other in moan peak-amplitude frequency (from 151-180 Hz) and grunt PRR (30.7-33.1 Hz). The moan peak-amplitude frequency was lowest in the largest male 02 and highest in the smallest male 03, suggesting a size-dependent mechanism of sound generation (as has been shown for grunt peak-amplitude frequency, but not moan peak-amplitude frequency, in *P. adspersus;* Crawford et al. 1997b). In most recordings the male 03 showed only two major components, near 180 Hz (H2, peak-amplitude frequency) and at about 409 Hz. We believe that the low intensity of those moans and poorer recording conditions compared to those of male 01 caused the appearance of H1 and H3/ H4 missing in this male's moans. Nevertheless, if an observed variability in sound characteristics were correlated with either genetic male quality or the provision of male parental care, female choice based on vocalisation parameters could explain part of the variability. However, for ascertaining intraspecific variability, a bigger sample size would be necessary.

In two *P. marianne* males, moan and grunt production was observed not only during obviously reproductive behaviours but also during escalating agonistic interactions long before spawning occurred, as well as when some larvae had already left the nest (sex of opponent unknown). Grunt PRR was lower than when females visited. Moans produced during fights showed brief frequency modulations that were not observed in reproductive contexts. Perhaps the sound producing "resonator" was mechanically affected by the butts of the opponent (see Figure 7, simultaneous butts and frequency modulations). Based on the characteristic spectral distribution of the moan in male 03 we believe that at least in that case the momentarily territorial male was also the only vocalising individual during agonistic interactions. After the fights both males continued their reproductive behaviours, suggesting that those fights did not directly affect the hierarchy within the group, or that both males were dominant over the intruder.

Sound production during territorial or agonistic behaviours of fishes is widespread (Ladich 1997), and was demonstrated also for mormyrids such as *Gnathonemus petersii,* which generates "click" sounds during intra- or interspecific interactions (Rigley & Marshall 1973), and *P. adspersus* generating "hoots" or "pops" during male-female agonistic interactions (Crawford et al. 1986). In *P. marianne* moans and grunts could have a dual function: (i) attraction of mates by signalling the male's motivational status and (ii) threatening competing males or potentially egg-eating females. The generation of sounds during key stages in the reproductive behaviour of male *P. marianne* indicates that vocalisations are of great behavioural relevance in this mormyrid species.

ACKNOWLEDGEMENTS

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