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# Sound production during courtship and spawning of *Oreochromis mossambicus*: male–female and male–male interactions

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The role of sound production of the Mozambique tilapia *Oreochromis mossambicus* in agonistic and mating interactions observed during hierarchy formation and in established groups was examined. Only territorial males produced sounds, during male–female and male–male courtship interactions and during pit-related activities (*e.g.* dig, hover and still in the nest). Sound production rate was positively correlated with courting rate. Although sounds in other cichlids are typically emitted in early stages of courtship, *O. mossambicus* produced sounds in all phases, but especially during late stages of courtship, including spawning. It is suggested that the acoustic emissions in this species may play a role in advertising the presence and spawning readiness of males and in synchronizing gamete release.

Key words: acoustic communication; Cichlidae; teleosts; territorial behaviour.

## INTRODUCTION

Sound production is widespread in teleosts and is observed in a variety of contexts, ranging from courtship (Lugli *et al.*, 1997) and agonistic interactions (Ladich, 1997) to competitive feeding (Amorim & Hawkins, 2000). Acoustic communication is especially prominent in territorial fishes and may play an important role in active territorial defence (Valinsky & Rigley, 1981; Ladich *et al.*, 1992), deterring intruders from territorial invasion (Myrberg, 1997), in species recognition (Myrberg *et al.*, 1978; Spanier, 1979) and in mate attraction (Myrberg *et al.*, 1986; Lugli *et al.*, 1996) and choice (Myrberg *et al.*, 1986).

The cichlids are an important group for the study of acoustic communication in fishes because of the widespread use of sounds during courtship and agonistic interactions (Lobel, 1998, 2001) and because of the potential involvement of acoustic communication in species recognition and mate choice behaviour, as shown in pomacentrids (Spanier, 1979; Myrberg *et al.*, 1986). Acoustic

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communication may explain the amazingly rapid speciation of cichlids (Stauffer *et al.*, 1995), but it has not been tested so far.

The Mozambique tilapia *Oreochromis mossambicus* (Peters) is an African maternal mouth-brooding cichlid. Males form dense nest aggregations (arenas or leks) during the mating season where they defend territories with nests (pits) to which they attract females. At the end of the mating sequence the male quivers while circling the nest followed by the female who takes both eggs and sperm into her mouth where the eggs are fertilized. After spawning, the female leaves the arena and during the next 20–22 days broods the embryos and fry in her mouth (Fryer & Iles, 1972). To establish social status and to obtain a territory, males have frequent agonistic interactions with other males to assess the competitive abilities of conspecifics and maintain dominance hierarchies. Mating success is highly correlated with social status (dominance). Territorial males frequently court other males that adopt a female-like behaviour and colouration (Oliveira & Canario, 2000). Oliveira & Almada (1998*a*) have suggested that male–male courtship in the Mozambique tilapia may be a by-product of a high level of sexual motivation, resulting in loss of sex discrimination by the courting male. Conversely, the courted males could gain prolonged presence in the arenas with a reduced level of attacks by the territorial males.

While most aspects of behaviour have been extensively studied in *O. mossambicus* (Baerends & Baerends van Roon, 1950; Neil, 1964; Turner, 1986; Oliveira & Canario, 2000), sound production has received little attention and existing studies have been brief, anecdotal and even contradictory. In the present work, the acoustic emissions of *O. mossambicus* were analysed and associated with behaviour during agonistic and mating interactions, both during group formation and in already established groups. Apart from the more traditional study of male–female mating interactions, the occurrence and context of sound emission during male–male courtship and spawning behaviour were investigated for the first time in teleosts.

## MATERIALS AND METHODS

### FISH

Fish were kept in mixed-sex groups in 200 l stock aerated aquaria with sand bottoms. Water was kept at 26 with a range of ±1° C, and photoperiod was 12L : 12D. Group size ranged from eight to 60 specimens depending on fish size (median = 16). Typically there were one to two territorial males per stock tank. Fish were fed with tropical fish commercial flakes. The studied specimens were raised in the Institut Superior de Psicologia Applicada's laboratory and were descendents from a stock kept in Aquário Vasco da Gama (Lisbon, Portugal) since the early 1970s originally caught in the Incomati River, Mozambique.

### SOUND MONITORING, RECORDING AND ANALYSIS

Sounds were recorded with a High Tech 94 SSQ hydrophone (sensitivity $-165$ dB re 1 V μPa$^{-1}$, frequency response within ±1 dB from 30 Hz to 6 kHz) placed just above the rim of a territorial male pit, connected to a DAT recorder (Sony TCD-D10 Pro). Aeration was stopped at least 15 min prior to sound monitoring or recording. Sounds were digitized at a rate of 22 kHz (16 bit resolution) and analysed with Canary 1.2.4 for Macintosh.

Because sounds were recorded in glass tanks, distortion of recorded sounds could be expected (Parvulescu, 1967). As the hydrophone was placed within the range of the attenuation length from the fish and the sound frequency range was lower than the minimum resonant frequency of the tank, as calculated after Okumura *et al.* (2002), the spectrum shape of the recorded sounds is probably accurate. Only the sounds that showed a clear structure were analysed.

The sounds made by *O. mossambicus* consisted of trains of low-frequency pulses organized in units of one or two pulses (single and double pulses; Fig. 1). The following sound parameters were measured: sound duration; number of pulse units, *i.e.* number of units that made up a sound (single and double pulses); pulse period, measured as the average peak to peak interval between consecutive pulse units in the entire sound; pulse duration; number of double pulses; double pulse period, defined as the interval between the two pulses measured peak to peak; duration of double pulses; peak frequency, defined as the frequency component with the highest energy in the entire sound; maximum frequency, maximum frequency measured for the whole sound. The temporal features were measured from the oscillograms and frequency parameters were obtained from the sonograms and the power spectra. Sonograms and power spectra were produced using the following parameters: filter bandwidth 349·7 Hz, FFT size 1024 points, time grid resolution 5·8 ms, 50% overlap, and a Hamming window.

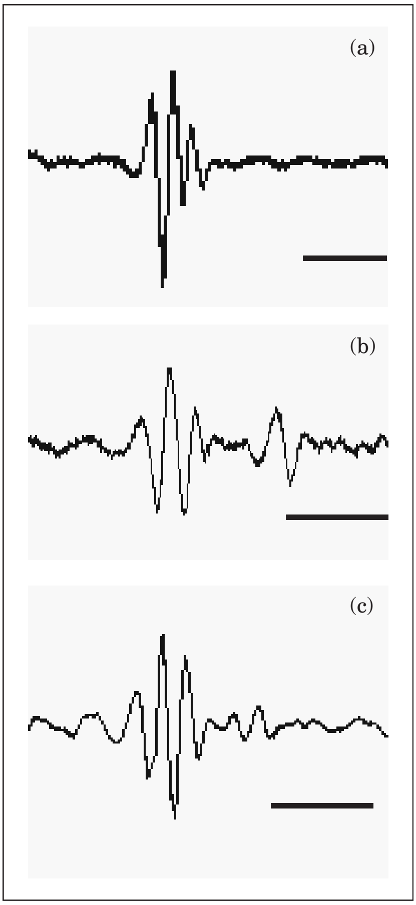

FIG. 1. Single (a) and double pulse (b, c) units in a drumming sound emitted by *Oreochromis mossambicus*. Double pulses may present a second pulse with almost similar (b) and with smaller (c) amplitude to the first pulse. Horizontal bar = 10 ms.

# THE CONTEXT OF SOUND PRODUCTION

## *Mixed-sex groups (stock tanks)*

The following behavioural patterns were identified in preliminary observations of social interactions and were considered in subsequent data recording: agonistic including charge, chase, bit, butting, lateral display, frontal display, tail beating, mouth fighting, pendelling, carouselling, male circling, flee and submission; courtship including approach, tilt, lead, circling the nest ('rolling' in Neil, 1964), tail wagging and quivering; pit-related activities (PRA) including dig, hover and still in the nest. The behavioural patterns are consistent with the descriptions given by Baerends & Baerends van Roon (1950), Neil (1964) and Oliveira & Almada (1998*a*), except for a newly identified behavioural pattern, still in the nest, that has been included in the species repertoire in the present study. During this pattern display the fish lays on the pit substratum motionless with unpaired fins lowered, usually after circling or digging and often emitting sounds.

Sound production and behavioural patterns were associated through focal observations (Martin & Bateson, 1993) of 13 territorial males, ranging in standard length ($L_S$) from 6·7 to 14·2 cm. The observer registered orally the sequence of behavioural actions performed by each focal fish on one track of the DAT recorder while any sounds produced by the fish were simultaneously recorded on a second track. An average of five recording sessions of 20 min each were achieved per fish (total of 68 sessions). The number of each behavioural act that occurred with and without sound production was scored. Sound was considered to be associated with a particular behaviour when it occurred during that behavioural act. This criterion was also used for all-male groups. The recorded sounds could unequivocally be attributed to the focal fish because the sound intensity varied accordingly to the subject's distance to the hydrophone.

Courtship rate, *i.e.* the number of courtship episodes min$^{-1}$, was scored and related to the sound production rate, defined as the number of sounds emitted min$^{-1}$. Any fish interaction involving at least one courtship pattern (see above) was counted as a courtship episode. Courtship episodes were classified as early-stage courtship, when tilt or lead occurred, and final-stage courtship, when tail wagging or quivering, were observed. These two groups of behavioural patterns are typical of the start or end of courtship sequences (Baerends & Baerends van Roon, 1950; Neil, 1964).

## *All-male groups*

All-male groups were formed, during which *O. mossambicus* interacted intensively for mutual assessment and hierarchy formation, followed by territorial establishment and courtship (Oliveira & Almada, 1998*b*). The purpose of this experiment was to promote agonistic interactions between males in order to check for sounds that are not often observed after the hierarchy among males is established. This study also aimed at testing whether sound production played any significant role in mutual assessment and hierarchy establishment in this species.

Sixteen males were individually isolated in 45 l aquaria for a week to minimize the possible effects of prior social experience (Chase *et al.*, 1994). After isolation four groups of four males were assembled in 200 l glass aquaria. To avoid any residence effects the four fish of each group were placed simultaneously in a tank. Fish size ($L_S$) differences within a group were small ($L_S$ ratio between the largest and smallest fish varied between 1·04 and 1·1). All males ranged in size between 12·0 and 13·6 cm $L_S$.

Ten observation sessions (15 min duration each) were performed in the three phases of group formation recognized by Oliveira & Almada (1998*b*), following a behaviour sampling procedure, *i.e.* all subjects were observed simultaneously and each occurrence of a particular behavioural act was recorded, together with details of which individuals were involved (Martin & Bateson, 1993). Two observation sessions were performed during the first phase, the second phase and during each of the 3 days of the third phase. All behavioural acts and the occurrence of simultaneous sound production were registered on separate channels of the DAT recorder, together with details on the individuals involved. The number of times each behavioural pattern occurred with and without sound emission was counted. To identify the onset of sound production during the dynamics of all-male group formation the frequency of agonistic, courtship and PRA were registered for each observation session. Agonistic interactions were classified as symmetrical or asymmetrical (depending on whether the receiver of the agonistic act retaliated or did not retaliate) since they are associated with mutual assessment and territorial defence, respectively (Oliveira & Almada, 1998*b*). In order to compare male–male courtship with the normal male–female courtship interactions, the courtship rate and sound production rate were also scored and compared with data of mixed-sex groups.

### THE ACOUSTIC REPERTOIRE

Sound recordings during focal observations of territorial males were not of sufficient quality to permit accurate sound descriptions, as vibrations of the laboratory building were passed on to the water of the aquaria. Nevertheless, the association of sound with behaviour was clear since the sounds were clearly recognized. To obtain better recordings a large aquarium (200 l) was placed on top of a layer of 50 cm of rockwool that absorbed the room structural vibrations. In this tank, a territorial male was placed with a female and allowed to court for 20 min. A pit was made in the middle of the tank with a hydrophone placed *c.* 6 cm above it. Usually the male used this pit to court and therefore their sounds were produced within 1–2 body lengths from the hydrophone. To increase female receptivity, ovulation was induced by an intraperitoneal injection of 200 μl saline containing 5 μg des-Gly 10, [D-Ala &]-LHRH ethylamide (Sigma) 48 h prior to the presentation to the male. A total of 19 males that individually courted the female were recorded. Male $L_S$ ranged from 8·4 to 12·9 cm. Water temperature was 27 ± 1° C.

### DATA ANALYSIS

The number of pulse units and sound duration were correlated with Spearman rank correlation tests. Sounds containing double pulses were compared to sounds made up of only single pulses with a discriminant analysis. The relation between sound parameters and fish $L_S$ was studied with regression analysis.

To associate behavioural actions with sound production, dependence between the variables, behavioural acts and sound emission (presence or absence), was tested with TESTMAT, a simulation programme based on a $\chi^2$ test (V.C. Almada, pers. comm.) that implements the algorithm of the programme ACTUS (Estabrook & Estabrook, 1989; Oliveira & Almada, 1998*a*), but allows larger tables. This test is preferable to a $\chi^2$ analysis when data does not follow the $\chi^2$ assumptions. It also has the advantage of indicating possible significant results for individual cells of the contingency table.

The hypothesis that sound could be categorized according to the associated behaviour was tested with a discriminant analysis using all the acoustic parameters. The following behavioural acts were considered: tilt, lead, tail wagging and still in the nest.

The number of early- and final-stage courtship episodes observed $\min^{-1}$ in mixed-sex groups was correlated with sound production rate with Spearman rank correlation tests. Courtship and sound production rates were compared between mixed-sex and all-male groups with Mann–Whitney *U*-tests.

## RESULTS

### THE ACOUSTIC REPERTOIRE

The sounds emitted by *O. mossambicus* were pulsed sounds with the main spectral components <750 Hz (Table I). All sounds contained a strong lower frequency component of *c.* 40 Hz [first component, peak frequency 1; Table I and Fig. 2(a)] that often masked the sound pulses (second component). This frequency peak is not common in sounds produced by fishes but the possibility

TABLE I. Descriptive statistics of the sounds produced by *Oreochromis mossambicus* in the present study. *n*, number of sounds analysed for all 19 studied males. An average of 21·2 sounds (S.D. = 11·7) were analysed per male

| | *n* | Mean | Min | Max | S.D. |
|---|---|---|---|---|---|
| Sound duration (ms) | 402 | 712·3 | 100·0 | 2833·5 | 457·7 |
| Number of pulse units | 402 | 16·8 | 4·0 | 60·0 | 8·7 |
| Pulse period (ms) | 402 | 44·2 | 21·5 | 136·5 | 14·0 |
| Pulse duration (ms) | 402 | 11·7 | 8·8 | 15·4 | 1·2 |
| Number of double pulse units | 402 | 1·4 | 0 | 24·0 | 3·2 |
| Double pulse period (ms) | 115 | 13·4 | 7·8 | 19·8 | 2·5 |
| Double pulse duration (ms) | 115 | 24·3 | 17·7 | 34·3 | 3·0 |
| Peak frequency 1 (Hz) | 385 | 37·6 | 25·0 | 54·0 | 4·4 |
| Peak frequency 2 (Hz) | 402 | 353·6 | 207·0 | 524·0 | 45·2 |
| Maximum frequency (Hz) | 402 | 750·1 | 520·0 | 1262·0 | 106·7 |

of it being an artefact of the recording environment and equipment seems very unlikely. Although there was some energy around 40 Hz in the background noise the acoustic energy markedly increased around this frequency when every sound was emitted. Furthermore, this frequency peak varied with $L_S$ (Fig. 3), was not related to any particular movement of the fish and was not present in recordings of other cichlid species' sounds (unpubl. data) carried out in similar-sized aquaria and recorded with the same equipment. Once the sounds were filtered (usually with a 170 Hz high-pass filter) the typical pulsed structure of fish sounds was clear [Fig. 2(b)]. The pulsed component of the signal peaked at a frequency of *c.* 350 Hz (peak frequency 2, Table I). Sound frequency significantly decreased with male $L_S$ (Fig. 3). The regression between the peak frequency 2 with male size showed the highest coefficient of determination ($r^2 = 0{\cdot}86$).

Sound duration and the number of pulse units were positively correlated (Spearman rank correlation, $n = 402$, $r = 0{\cdot}89$, $P < 0{\cdot}001$, Fig. 4). Around 25% of the analysed sounds were double pulses (Table I). Not all pulses in these sounds, however, showed a double structure and double pulses were not always alike: sometimes the second pulse showed similar amplitude to the first pulse [Fig. 1(b)], whereas in other cases the second pulse had a much lower amplitude [Fig. 1(c)]. In the latter case, the second pulse resembled the sound pressure change related to the relaxation phase of the sound-producing muscle as described for the toadfish *Opsanus tau* (L.) (Skoglund, 1961). The possibility that the second pulse may be an acoustic artefact from the recording environment should not be excluded. The results of the discriminant analysis showed that the sounds of *O. mossambicus* could not be classified into two types based on the presence of double pulse units. Only 5% of the sounds containing double pulses were correctly classified.

## THE CONTEXT OF SOUND PRODUCTION

### *Mixed-sex groups*

Only territorial males, *i.e.* males that actively dug and defended their nest, showing black colouration (Neil, 1964), were heard to produce sounds. In some

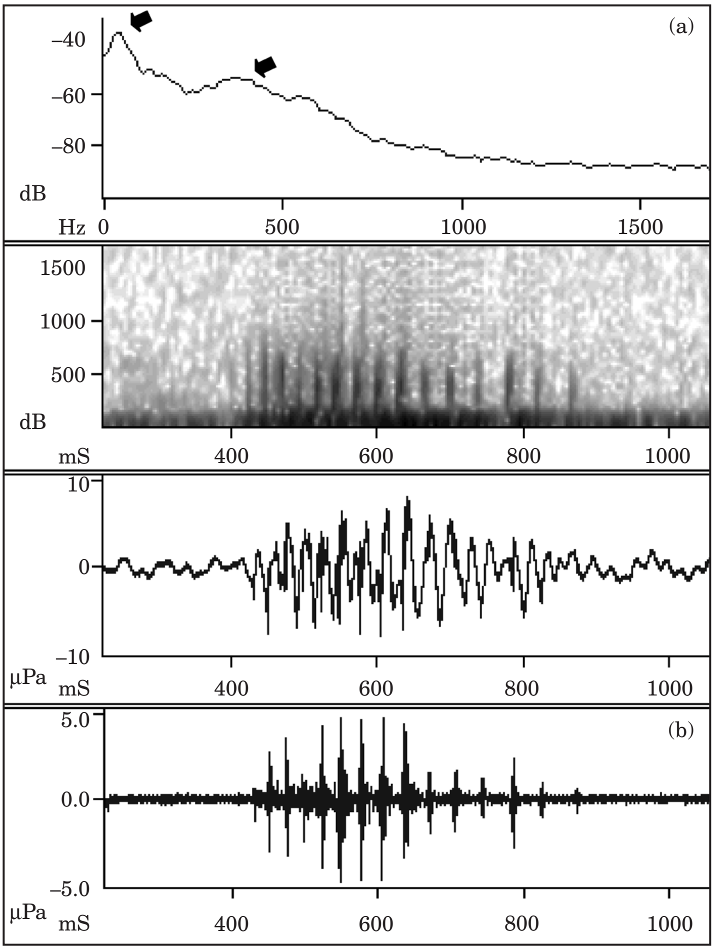

FIG. 2. (a) Spectrum (top), sonogram (middle) and oscillogram (bottom) of a sound produced by male *Oreochromis mossambicus*. ➡, Frequency peaks at 38 and 378 Hz. (b) Oscillogram of the same sound filtered with a 170 Hz high-pass filter.

cases, semi-territorial individuals that stayed in the water column presenting a light-dark colouration occupied the pit of a temporarily absent dominant male and courted nearby females also producing sounds. Sneaking males that entered the nest of a dominant male during a spawning episode exhibiting quivering behaviour, did not emit sounds (Oliveira & Almada, 1998*a*). Sound production was significantly associated with the behavioural patterns: tilt, tail wagging, quivering and still in the nest (Table II). Tail wagging was the only behaviour nearly always accompanied by sound emissions (90%, Table III). Agonistic interactions were often observed in mixed-sex groups (26% of all acts observed), but were performed silently.

Pulse period and number of pulse units were the variables that could best discriminate between sounds associated with different behavioural acts (discriminant analysis, $n = 366$, Wilks' $\lambda = 0{\cdot}739$; $F_{18,973} = 6{\cdot}10$, $P < 0{\cdot}001$). Only the

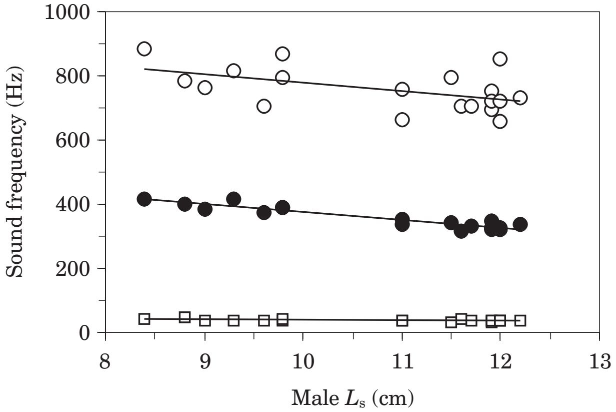

FIG. 3. Relation between peak frequency 1 (□, $y = 59.08 - 2.00x$, $r^2 = 0.50$, $P < 0.001$), peak frequency 2 (●, $y = 623.64 - 24.83x$, $r^2 = 0.88$, $P < 0.001$) and maximum frequency (○, $y = 1043.4 - 26.49x$, $r^2 = 0.27$, $P < 0.05$) of courtship sounds with male standard length ($n = 19$).

sounds associated with tail wagging, which presented higher pulse rate and number, however, showed a high percentage of correct classifications (Table IV).

The focal males in mixed-sex groups performed a mean ± S.D. of 1·9 ± 0·35 courtship episodes $\text{min}^{-1}$ ($n = 13$) and emitted sounds at a rate of 1·1 ± 0·7 sounds $\text{min}^{-1}$ ($n = 13$). The rate of acoustic emissions registered in an observation session was significantly correlated with the rate of final-stage courtship episodes (Spearman rank correlation, $n = 13$, $r = 0.71$, $P < 0.01$) but not with the rate of early-stage courtship episodes ($P > 0.05$). The rate of final- and early-stage courtship episodes was uncorrelated ($P > 0.05$).

### *All-male groups*

The dynamics of social interactions and sound emissions during group formation are shown in Fig. 5. Symmetrical fights were more frequent during the first phase of group formation and decreased thereafter, but the amount of asymmetrical fights remained approximately constant throughout the study

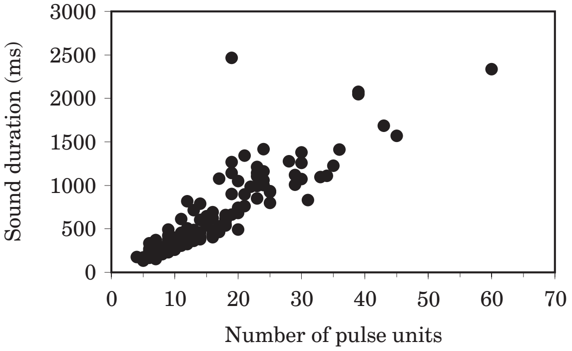

FIG. 4. Relation between number of pulse units and sound duration.

TABLE II. Association of sound emissions with the social behaviour observed in mixed-sex and all-male groups. Probabilities are given by the programme TESTMAT. ***$P<0{\cdot}001$; **$P<0{\cdot}01$; *$P<0{\cdot}05$; NS, not significant. The values in parentheses are the observed values for each table cell. Total $n$ (mixed-sex groups) $=10\,676$ and total $n$ (all-male groups) $=3978$. Agon. asym, asymmetrical agonistic behaviour; agon. sym, symmetrical agonistic behaviour; Circ, circling the nest; TW, tail wagging; Q, quivering; Hov, hover; Nest, still in the nest

| | Mixed-sex groups | | All-male groups | |
|---|---|---|---|---|
| Behavioural patterns | Without sound | With sound | Without sound | With sound |
| Agonistic | ***<br>(2734) | NS<br>(11) | Agon. asym<br>***<br>(2200)<br>Agon. sym<br>*<br>(834) | Agon. asym<br>NS<br>(20)<br>Agon. sym<br>NS<br>(0) |
| Tilt | NS<br>(1201) | ***<br>(358) | NS<br>(49) | ***<br>(81) |
| Lead | NS<br>(904) | NS<br>(152) | NS<br>(51) | **<br>(17) |
| Circ | *<br>(1099) | NS<br>(94) | NS<br>(192) | **<br>(26) |
| TW | NS<br>(43) | ***<br>(374) | NS<br>(5) | ***<br>(9) |
| Q | NS<br>(241) | ***<br>(146) | — | — |
| Hov | ***<br>(1156) | NS<br>(19) | NS<br>(72) | NS<br>(9) |
| Nest | NS<br>(121) | ***<br>(89) | NS<br>(24) | ***<br>(73) |
| Dig | *<br>(1215) | NS<br>(100) | NS<br>(278) | **<br>(38) |
| Approach female | **<br>(596) | NS<br>(23) | — | — |

[Fig. 5(a)]. Courtship behaviour, PRA and the presence of territorial males were observed during the second phase of group formation [Fig. 5(b)]. Sound production was only registered after territorial behaviour was observed and dominance hierarchies were established among fish [Fig. 5(b)].

The probability of symmetrical and asymmetrical agonistic behaviour being performed without sound production was significantly high. Sound production, however, was significantly associated with the behavioural patterns: still in the nest, dig, circle, tilt, lead and tail wagging (Table II). Still in the nest, tail wagging and tilt were the actions more frequently accompanied by sound emissions (Table III).

Courtship rate in the third phase of all-male group formation was on average $0{\cdot}8\pm0{\cdot}5$ courtship episodes $\text{min}^{-1}$ ($n=4$), and sound production rate in the same phase averaged $1{\cdot}0\pm1{\cdot}0$ sounds $\text{min}^{-1}$ ($n=4$). Courtship rate in all-male

TABLE III. Frequency of co-occurrence of behaviour and sound in mixed-sex and all-male groups. Agon. asym, asymmetrical agonistic behaviour; agon. sym, symmetrical agonistic behaviour; Circ, circling the nest; TW, tail wagging; Q, quivering; Hov, hover; Nest, still in the nest

| Behavioural patterns | Mixed-sex groups | All-male groups |
|---|---|---|
| Agonistic | 0·4 | Agon. asym<br>0·9<br>Agon. sym<br>0·0 |
| Approach female | 3·7 | — |
| Tilt | 23·0 | 62·3 |
| Lead | 14·4 | 25·0 |
| Circ | 7·9 | 11·9 |
| TW | 89·7 | 64·3 |
| Q | 37·7 | — |
| Hov | 1·6 | 11·1 |
| Nest | 42·4 | 75·3 |
| Dig | 7·6 | 12·0 |

groups was significantly lower than in mixed-sex groups (Mann–Whitney $U$-test, $U = 3{\cdot}0$, $P < 0{\cdot}01$) but no differences were found for sound production rate ($P > 0{\cdot}05$).

Courtship behaviour directed towards males and females showed some qualitative differences. When a male performed a tilt directed to another male its body was less inclined and the unpaired fins were erected, looking like an intermediate behaviour between a tilt and a lateral display. Likewise the acts lead and tail wagging were made with partially or fully erected unpaired fins. The courted male showed various responses ranging from fleeing to typical female sexual behaviour, including inhaling sperm released by the quivering (dominant) male as described in Oliveira & Almada (1998*a*).

## DISCUSSION

The occurrence of sound production in *O. mossambicus* was studied during male–female and male–male agonistic and courtship interactions. Only

TABLE IV. Classification matrix of the courtship sounds associated with different behavioural categories (discriminant analysis)

| Sound categories | *n* | % of correct classification |
|---|---|---|
| Tilt | 71 | 50 |
| Lead | 107 | 18 |
| Tail wagging | 143 | 86 |
| Still in the nest | 45 | 0 |
| Total | 366 | 49 |

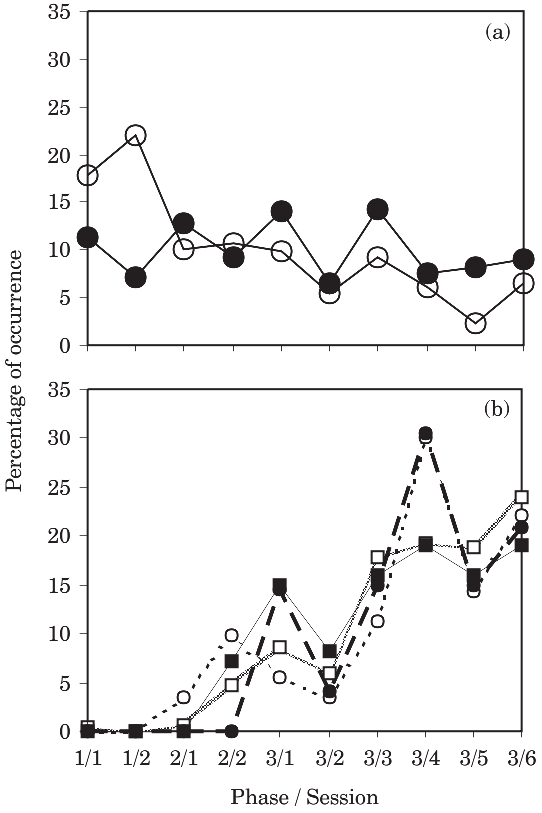

FIG. 5. Dynamics of social behaviour and sound production during group formation in all-male groups. Data are average values for the four studied groups and refer to the proportion of each behavioural category and number of territorial males observed in each phase of group formation (Oliveira & Almada, 1998*b*) and recording session. (a) Agon. sim (●), symmetrical agonistic behaviour and agon. asym (○), asymmetrical agonistic behaviour. (b) PRA (□), pit-related activities (still in the nest, hover and dig), T (■), number of territorial males, court (- -○- -), courtship behaviour and sound production (–●–).

territorial males produced one type of low-pitch sounds during courtship and PRA. These sounds are similar to the ones previously described for this species (Table V) and for other cichlids, except for the presence of a strong frequency component peaking at *c.* 40 Hz besides the more typical one at 350 Hz (Tables I and V). The mechanism for producing low-frequency sounds in *O. mossambicus* and other cichlids is unknown but it has been suggested that they could be made by the pharyngeal teeth (Lobel, 2001) and amplified by the swim bladder (Brown & Marshall, 1978; Lobel, 2001).

Lanzing (1974) has described stridulation sounds made by the Mozambique tilapia and suggested they have a communicatory function (Table V). In the present study, males and females emitted these high-pitched sounds constantly but they were interpreted as being the result of sand grains moving against the pharyngeal teeth as suggested by Rodman (1966).

In mixed-sex groups, the emission of drumming sounds was significantly associated with acts of all stages of courtship, including spawning and PRA.

TABLE V. Previous descriptions of the sounds produced by *Oreochromis mossambicus* and associated context

| Author | Sound description | Sound duration | Number of pulses | Pulse duration | Pulse period | Frequency | Context |
|---|---|---|---|---|---|---|---|
| Konstantinova *et al.* (1979) | Growl | — | 7–18 double pulses | 7–10 ms | 35–100 ms | Fundamental: 200–250 Hz | Courtship |
| Konstantinova *et al.* (1979) | Rattle | — | 2–12 single | 6–12 ms | 7–95 ms | Range: 200–250 Hz | Courtship |
| Konstantinova *et al.* (1979) | Puffing | — | 4–6 single | 25–30 ms | 100–250 ms | Range: 185–250 Hz | Courtship |
| Konstantinova *et al.* (1979) | Aggressive sound | 50–500 ms | — | — | — | Range: 120–1400 Hz | Agonistic |
| Rodman (1966) | Low-frequency sound | 0·6 s | Double pulses (no.?) | Double pulse duration: 0·02 s | — | Range: 50–600 Hz | Agonistic |
| Lanzing (1974) | High-pitched sound | 100–250 ms | — | 5 ms | — | Range: 1–16 kHz | Agonistic and other |
| Marshall (1971) | Low-pitched drumming sound | — | — | — | — | — | Courtship and parental care |

Sample size was not given for any of the studies.

The behaviour most likely to be accompanied by acoustic emissions was tail wagging, a behavioural pattern that occurs typically close to spawning. In cichlids, acoustic emissions made during courtship are usually associated with quivering, a behavioural act typical of early courtship stages (McElroy & Kornfield, 1990). In *O. mossambicus* quivering is performed by males while releasing milt (Baerends & Baerends van Roon, 1950; Neil, 1964). *Sarotherodon galilaeus* (L.) and *Herotilapia multispinosa* (Günther) also produce sounds close to spawning (Brown & Marshall, 1978), but there is no report of sounds emitted during spawning in cichlids. Sound production during prespawning activities is a widespread phenomenon in fishes but relatively rare during spawning. Vocalizations made during spawning have only been reported for five species of teleosts (Lobel, 1992; Lobel & Mann, 1995; Lugli *et al.*, 1995). Sounds produced just prior to or during spawning are thought to play a major role in synchronizing gamete release (Lobel, 1992; Hawkins & Amorim, 2000).

The emission of acoustic signals during courtship may serve to advertise the presence and reproductive readiness of the male sender to the females as suggested for other fishes (Hawkins, 1993). Courtship rate in *O. mossambicus* is known to be positively correlated with dominant indexes, androgen levels (after all-male group formation) and nest volume, and females prefer males with larger nests which also tend to have higher gonado-somatic indices (Oliveira & Canario, 2000). Given that in *O. mossambicus* the rate of acoustic emissions increased with the rate of final-stage courtship episodes, it is plausible that females could be able to judge male status and spawning readiness by listening to sound production rate alone. Additional cues could be given by the lower sound peak frequencies (characteristic of larger males), higher pulse rate and number (associated with tail wagging sounds), and by nest size and behaviour.

Sounds produced by fish during male–male courtship are reported here for the first time. All-male groups presented a lower courtship rate but sound production rate did not differ from mixed-sex groups (male–female courtship interactions). Based on the present results, it is proposed that the courted males could gain not only prolonged presence in the arenas with a reduced level of attacks by the territorial males as suggested by Oliveira & Almada (1998*a*), but also additional information on the dominant male spawning readiness from listening to the sound production rate. If so, subordinate males could use this information to approach the territorial male closest to spawning in the arena and act as sneakers.

In the present study, a large number of male–male and male–female agonistic interactions were observed and agonistic acts were nearly always made in silence. In all-male group formation sound production was neither important for male mutual assessment (symmetrical agonistic interactions) and the establishment of dominance relations, nor for territorial defence (asymmetrical agonistic interactions). Instead, the emission of sounds was heard only after hierarchy establishment and the presence of a territorial male in the group. It is possible that the full acoustic context in this species was not observed but this study strongly suggests that the main role of acoustic communication in *O. mossambicus* takes place during courtship and spawning. Further investigation involving playback experiments is needed to study the use of courtship acoustic signals by females and competitive males.

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