

# 1 Courtship and agonistic sounds by the cichlid fish

## 2 *Pseudotropheus zebra*

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11 Courtship and agonistic interactions in an African cichlid species present a richer diversity of  
12 acoustic stimuli than previously reported. Male cichlids, including those from the genus  
13 *Pseudotropheus* (*P.*), produce low frequency short pulsed sounds during courtship. Sounds emitted  
14 by *P. zebra* males in the early stages of courtship (during quiver) were found to be significantly  
15 longer and with a higher number of pulses than sounds produced in later stages. During agonistic  
16 intrasexual quiver displays, males produced significantly longer sounds with more pulses than  
17 females. Also, male sounds had a shorter duration and pulse period in courtship than in male–male  
18 interactions. Taken together, these results show that the acoustic repertoire of this species is larger  
19 than what was previously known and emphasize the importance of further research exploiting the  
20 role of acoustic stimuli in intra- and interspecific communication in African cichlids. © 2008  
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### 24 I. INTRODUCTION

25 In recent years much attention has focused on the role of  
26 interspecific mate choice on the impressive rate of speciation  
27 of cichlid fishes from the Great African Lakes that have un-  
28 dergone some of the fastest and most extensive adaptive ra-  
29 diations among vertebrates (e.g., Turner, 1999; Albertson *et*  
30 *al.*, 2003). Many authors have proposed that sexual selection  
31 driven by female choice acting on male courtship colors may  
32 have been a significant factor on the rapid speciation of these  
33 fishes (e.g., Couldridge and Alexander, 2001; Genner and  
34 Turner, 2005). Males of several African cichlid fishes are  
35 known to produce sounds during courtship [reviewed in Lo-  
36 bel (1998) and Amorim (2006)] and recently acoustic signal-  
37 ing has also been pointed out as a possible mechanism in-  
38 volved in reproductive isolation (Lobel, 1998; Amorim *et al.*,  
39 2004) among African Great Lake cichlids.

AQ: #1 40 Less attention has been given to the role of acoustic  
41 communication in intraspecific mate choice in these fishes.  
42 In the early stages of courtship, male *Pseudotropheus* (*P.*)  
43 quiver to females, producing low-frequency short-pulsed  
44 sounds (Amorim *et al.*, 2004), but there are no published  
45 records of sound production associated with behavioral ele-  
46 ments characteristic of the later stages of courtship (Baerends  
47 and Baerends van Roon, 1950), or during agonistic displays.  
48 If there is sufficient intraspecific variability in sound produc-  
49 tion then acoustic communication may play a role in intra-  
50 and intersexual selection and influence the outcome of fights

and mating decisions in *Pseudotropheus*, as observed in 51  
other animals (e.g., Ladich *et al.*, 1992). 52

The present study was aimed at investigating the full 53  
acoustic repertoire of *P. zebra* males and females associated 54  
with both courtship and agonistic contexts. 55

### II. METHODS 56

#### A. Fish stocks and maintenance 57

Twenty adult male and twelve adult female first- 58  
generation offspring bred from a stock of wild-caught adult 59  
*Pseudotropheus zebra* from Nkhata Bay, Malawi (11°36' N; 60  
34°17' E) were used in this study. After each trial, the fish 61  
were returned to stock tanks. Each tank was fitted with an 62  
external power filter and maintained at 25–27 °C by an in- 63  
ternal 250-W heater, on a 12:12 h light:dark cycle provided 64  
by room lights. A third of the tank's water (pH 7.5–8.5) was 65  
changed weekly. Fish were fed twice daily with a mixture of 66  
commercial cichlid sticks and koi pellets. 67

#### B. Experimental protocol 68

Experiments were conducted between January and Sep- 69  
tember 2005. Trials were conducted in two aquaria (120 70  
×60×45 cm high) placed on top of a concrete plate sup- 71  
ported by two rockwool blocks (100×50×30 cm). This 72  
setup proved to be effective to minimize external noise trans- 73  
mitted through the building improving considerably noise to 74  
signal ratio at the low frequencies considered in this study 75  
(Fig. 1). Each experimental tank was divided transversally 76

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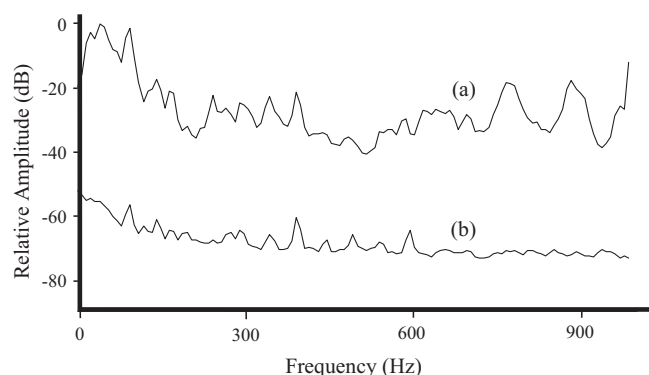


FIG. 1. Comparison between spectra of laboratory background noise recorded in (a) a stock tank, placed on top of a thin layer (2 cm) of expanded polystyrene and in (b) an experimental tank, placed on top of a thick layer (50 cm) of rockwool. Amplitude levels (dB) are relative to the maximum value of the spectra. Sampling frequency 48 kHz, 2048 point FFT, filter bandwidth 15 Hz, Hamming window, and 50% overlap.

physical contact, including biting (Baerends and Baerends van Roon, 1950). During lateral displays, animals often quiver, a behavior that is similar to the courtship quiver. To avoid physical injuries, fish were separated before or at the first sign of escalation to physical contact.

Recordings lasted 10 min for female–female, 15 min for male–male, and 20 min for male–female interactions. The duration of the recording sessions was derived from preliminary observations. All individuals were identified by natural features, such as number and position of eggspots, fin length, and marks on the body and fins.

### C. Sound recording and analysis

Sounds were recorded using two High Tech 94 SSQ hydrophones (sensitivity of  $-165$  dB re  $1$  V  $\mu\text{Pa}^{-1}$ , flat frequency response  $\pm 1$  dB up to 6 kHz) and a Pioneer DVD Recorder DVR-3100 ( $\pm 1.5$  dB from 40 Hz to 2 kHz, sampled at 48 kHz, 16 bit). One hydrophone was placed above the terracotta pot, where the territorial individuals would most likely exhibit courtship or agonistic behaviors. A second hydrophone was placed in the middle of the main compartment or in the location where individuals would more actively display at each other. The use of two hydrophones improved the probability of recording sounds close to the sound producer and also provided information on the degradation of the acoustic signals with distance. Recorded sounds could be attributed to the subject males because their intensity varied with distance from the hydrophones and were consistently associated with particular courtship displays.

Sounds were analyzed with Adobe Audition 2.0. (Adobe Systems Inc., 2005) and Raven 1.2.1 for Windows (Cornell Lab of Ornithology, 2003). Only sounds that showed a clear structure and a high signal-to-noise ratio were considered. These were typically recorded at a distance of 1–2 body lengths of the focal fish. The acoustic parameters analyzed (Fig. 2) were sound duration; number of pulses in a sound; mean pulse period of the entire sound (Mean PP); and sound-peak frequency (for a description of the acoustic parameters see Amorim *et al.*, 2004). In addition, other parameters also considered included the mean pulse period of the first five pulses in a sound (Initial PP), and a second previously undetected sound-peak frequency (PF1) typically around 150 Hz, which is of higher energy than the sound peak in the 450 Hz region (PF2) described by Amorim *et al.* (2004). PF1 is easily confounded with background noise if the recording aquarium is insufficiently acoustically insulated. When comparing an uninsulated stock tank with the experimental tanks, background noises differed by approximately 50 dB at 100 Hz, i.e., around the frequency region of PF1, and by 30 dB at 450 Hz, i.e., around the frequency of PF2 (Fig. 1). Temporal features were measured from oscillograms and sound peak frequencies from power spectra based on 2048 point FFT with a Hamming window applied. Data are presented in relative units as it was not possible to measure absolute sound levels.

Statistical analyses were performed using Statistica 7.0 (StatSoft Inc., 2005). Nonparametric statistics were used

by two opaque removable partitions into three compartments: one of 50 cm in the middle and two of 35 cm.

During courtship experiments, a single male was introduced into each of the smaller lateral compartments. These compartments were provided with terracotta pots that served as refuges and prospective spawning sites. In the central compartment, six or seven females were kept permanently. Males were left visually isolated to acclimatize for a minimum of 36 h prior to the beginning of the recordings. This period was required for males to become territorial, as shown by “digging” behavior around the refuge. Before the recording period, all electrical devices were switched off, apart from the room lights. Then, one of the opaque partitions was removed, and one male had free access to the females in the central compartment. During courtship behavior, male *P. zebra* perform a number of distinct types of displays to the females, which are not always shown in a fixed order. These include the behavioral patterns dart, quiver, lead swim, and circling with the female (Baerends and Baerends van Roon, 1950; Amorim *et al.*, 2004). Although recording, we noted which visual displays were accompanied by sound production. However, sometimes males would produce sounds when not performing any behavioral display, such as during swimming or when standing still in the water column. Once recording was complete, the tested subject was weighed (wet mass, M), measured (standard length, SL) and returned to a stock tank. Only 12 males and 5 females emitted sounds suitable for analysis. Male size averaged 107.1 mm SL [ $\pm$ SD (range) =  $\pm 11.8$  (88.0–122.0) mm, where SD is standard deviation] and 40.5 g M [ $\pm 9.7$  (22.0–57.7) g], whereas females averaged 103.6 mm SL [ $\pm 0.02$  (100.0–106.5) mm] and 30.4 g M [ $\pm 2.5$  (27.4–33.5) g].

Sounds from females were recorded from female–female interactions that naturally occurred when they were in the middle compartment isolated from the males. Sounds from male–male interactions were recorded by placing another male in the middle compartment (instead of the females), and following a similar procedure to the courtship sound recordings. Agonistic encounters consisted of frontal and lateral displays and chasing, occasionally escalating to

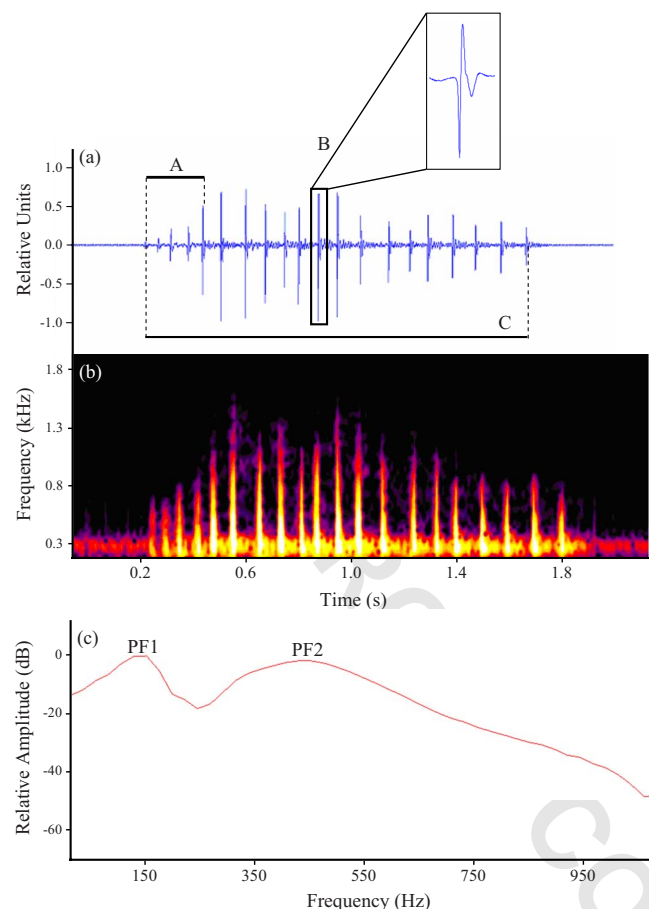


FIG. 2. (Color online) (a) Oscillogram, (b) sonogram, and (c) power spectrum of a *Pseudotropheus zebra* male courtship sound, representing some of the acoustic parameters measured: mean pulse period of the (A) first five pulses, (B) is an example of a pulse number of pulses, and (C) sound duration in (a) and peak frequency 1 (PF1) and 2 (PF2) in (c). Sampling frequency 48 kHz, 2048 point FFT, filter bandwidth 15 Hz, Hamming window, and 50% overlap.

174 whenever the assumptions for parametric tests were not met  
175 after applying data transformations. One-way analysis of  
176 variance (ANOVA) was used to compare differences among  
177 means of the acoustic parameters of male courtship quiver  
178 sounds. The square root transformation was applied to the  
179 number of pulses to meet the ANOVA assumptions. Spear-  
180 man rank correlation was used to estimate whether courtship  
181 quiver sound parameters were related to male morphological  
182 features (standard length, weight, and number of eggspots).  
183 Twelve males with an average of 17 sounds per male ( $\pm 12.1$   
184 SD) were considered for these analyses.

185 The Kruskal–Wallis nonparametric test was used to  
186 compare the acoustic characteristics of sounds produced dur-  
187 ing different stages of courtship (lead swim, quiver, no visual  
188 display, and circle). Because few interactions proceeded to  
189 late stages of courtship, relatively few sounds were recorded  
190 during activities characteristic of such phases. The following  
191 sample sizes were considered: 36 quiver sounds from 9  
192 males; 12 lead-swim sounds from 5 males; 10 circle sounds  
193 from 1 male; and 8 no display sounds from 4 males. Note  
194 that in this analysis, data concerning quiver sounds were re-  
195 stricted to 36 randomly selected sounds from 9 males from  
196 the whole data set (i.e., 4 sounds per each male), to avoid

large imbalances between factor levels sample sizes. Circling  
sounds were extremely hard to record, not only due to the  
fact that this species rarely got to the ending stages of court-  
ship during trials, but also because circling did not always  
occur near the hydrophone. Thus, even though a few other  
circling interactions were observed, it was possible in only  
one case to analyze their uttered sounds. Nevertheless, the  
comparison between circling and other sounds seemed nec-  
essary to ascertain the variability in the acoustic repertoire of  
this species and was included for analyses. *Post-hoc* pairwise  
comparisons were made with Dunn tests to determine differ-  
ences between groups of courtship behaviors (Zar, 1984).

The hypothesis that sounds produced by males when  
courting females could be different from those produced by  
both sexes during agonistic interactions was also tested with  
one-way ANOVA. For these analyses, 198 courtship quiver  
sounds from the 12 analyzed males (i.e., all quiver sounds  
recorded during courtship interactions), as well as 124 ago-  
nistic sounds emitted by 9 males and 27 sounds produced in  
agonistic contexts by 5 females were considered. An average  
of 14 sounds ( $\pm 4.4$ ) and 5 sounds ( $\pm 2.1$ ) were considered  
per male and per female, respectively, in agonistic contexts.  
The square root transformation was applied to the number of  
pulses, whereas logarithmic transformations were carried out  
for sound duration and the mean pulse period of the first five  
pulses to meet the requirements of normality and homosce-  
dasticity. Because PF2 is correlated with male SL (see Sec.  
III), an analysis of covariance (ANCOVA) was used to com-  
pare this frequency parameter among sexes and social con-  
text, having fish SL as a covariate to control for the effect of  
male size. *Post-hoc* pairwise comparisons were made with  
Tukey tests for unequal sample sizes.

### III. RESULTS

#### A. Male courtship sounds

During intersexual courtship trials, female sounds were  
not detected. Focal male *Pseudotropheus zebra* varied in  
their tendency to court females. Sounds were more fre-  
quently produced when individuals from both sexes showed  
a greater courtship activity. Eight of the twenty males tested  
neither attempted courtship nor produced any sound suitable  
for analysis. Only four males displayed late-stage courtship  
behavior. Most recorded sounds (86.4%) were produced by  
males during quivering, the main early stage courtship be-  
havior. Because few encounters proceeded to the late stages  
of courtship, such as lead swim and circle, there was a rela-  
tively scarce sample (13.2%) of sounds produced during final  
courtship.

Male quiver sounds had two main sound-peak frequen-  
cies at approximately 150 Hz (PF1) and 450 Hz (PF2). The  
mean quiver sound duration was around 700 ms with ap-  
proximately 9 pulses per sound. The mean pulse period was  
approximately 90 ms and the initial pulse period circa 80 ms.  
There were significant differences between males in all sonic  
characteristics measured, except for sound duration (Table I).  
Intraindividual variation was generally high, especially for  
sound duration and number of pulses and lowest for PF1 and  
PF2, as shown by their coefficients of variation (Table I).



TABLE I. Characteristics of sounds produced by *P. zebra* males and females during quiver in inter- and intrasexual interactions (male–female—courtship interactions; male–male and female–female—agonistic interactions). Means, SD, and range are based on fish means. Coefficients of variation (COV = SD/mean × 100) represent intraindividual variability of the acoustic parameters. Results for one-way ANOVA testing differences between males for courtship quiver acoustic parameters, and testing differences between sounds made during different contexts and gender are presented.

Sound parameters	Male–female		Male–Male		Female–female		Differences between males (courtship quiver)		Differences between contexts/gender	
	Mean ± SD (range)	COV (%)	Mean ± SD (range)	COV (%)	Mean ± SD (range)	COV (%)	$F_{11,186}$	$P$	$F_{2,23}$	$P$
Duration (ms)	671.7 ± 135.59 (421.4–856.8)	60.37	960.5 ± 295.29 (549.1–1429.5)	69.13	524.2 ± 152.95 (358.3–732.6)	72.00	0.87	ns	8.56 <sup>c</sup>	0.002
Number of pulses	8.6 ± 1.67 (6.6–12.4)	51.23	8.7 ± 3.48 (4.7–13.8)	52.59	4.9 ± 0.99 (3.8–6.3)	52.46	1.86 <sup>a</sup>	0.047	6.16 <sup>a</sup>	0.007
Mean pulse period (ms)	86.8 ± 14.37 (67.5–113.3)	22.32	125.7 ± 23.91 (90.1–160.9)	36.39	123.8 ± 27.06 (92.9–165.3)	39.83	3.69	<0.001	11.10	<0.001
Initial pulse period (ms)	76.7 ± 15.31 (52.1–103.6)	26.43	110.8 ± 27.97 (79.2–149.8)	34.64	116.7 ± 34.52 (91.7–176.4)	41.15	3.77	<0.001	8.45 <sup>c</sup>	0.002
PF1 (Hz)	155.6 ± 26.20 (129.4–220.7)	15.17	138.0 ± 14.97 (117.2–164.1)	5.99	143.1 ± 6.72 (133.9–152.3)	8.33	10.80	<0.001	2.04	ns
PF 2 (Hz)	488.8 ± 40.84 (423.9–557.8)	8.77	462.9 ± 35.40 (433.6–550.8)	6.06	480.2 ± 29.14 (445.3–525.0)	8.05	8.13 <sup>b</sup>	<0.001	1.80 <sup>b</sup>	ns

Squared root transformation is applied. Results from ANCOVA using fish SL as a covariate. Logarithmic transformation is applied.

254 Larger males produced quiver courtship sounds with  
 255 lower frequencies at PF2 (mass:  $r_s = -0.62$ ,  $N = 12$ ,  $P$   
 256  $= 0.028$ ; length:  $r_s = -0.81$ ,  $N = 12$ ,  $P = 0.001$ ). Eggspot num-  
 257 ber was not significantly related to male size (M and SL:  
 258  $r_s = 0.50$ ,  $P > 0.05$ ). Males with larger number of eggspots  
 259 tended to make calls with lower PF1 frequencies ( $r_s = -0.82$ ,  
 260  $N = 9$ ,  $P = 0.001$ ) and higher pulse repetition rates, i.e., shorter  
 261 pulse periods (mean pulse period:  $r_s = -0.68$ ,  $N = 9$ ,  $P = 0.04$ ).  
 262 The duration of sounds and their number of pulses dif-  
 263 fered according to the courtship behavior performed by the  
 264 males with longer sounds containing more pulses emitted  
 265 during quivering bouts (Table II, Fig. 3). The mean pulse  
 266 period of the first five pulses was shorter in sounds associ-  
 267 ated with quivering than in sounds registered when males

were not displaying, with lead-swim and circle sounds being 268  
 intermediate (Table II, Fig. 3). The PF1 also differed signifi- 269  
 cantly according to which behavior the sound was associated 270  
 with (Table II), but Dunn tests were unable to distinguish any 271  
 pair of behavioral categories. 272

### B. Agonistic sounds 273

Sound production by males during agonistic interactions 274  
 frequently occurred after a brief fight, where males would 275  
 silently display frontally or laterally. Following such a con- 276  
 test, the dominant male (normally the resident or the larger 277  
 fish) displayed laterally and quivered to the submissive male. 278  
 Submissive males rapidly lost their bright colors, becoming 279

TABLE II. Characteristics of courtship sounds made by *P. zebra* during lead swim, quiver, with no associated display and circle. Data are pooled for all recorded individuals due to the small sample size (for quiver sounds only a subsample of 4 sounds per male was considered in the analyses—see Sec. II). Coefficients of variation are also given: COV = SD/mean × 100. Results for Kruskal–Wallis statistics testing differences between sounds associated with different courtship behaviors are presented.

Sound parameters	Lead swim		Quiver		No display		Circle		Kruskal–Wallis	
	Mean ± SD (range)	COV (%)	Mean ± SD (range)	COV (%)	Mean ± SD (range)	COV (%)	Mean ± SD (range)	COV (%)	$H$	$P$
Duration (ms)	567.3 ± 247.14 (214.0–1210.0)	43.6	1198.6 ± 647.32 (298.0–2622.0)	54.0	481.4 ± 381.16 (201.0–1276.0)	79.2	561.7 ± 157.44 (343.0–853.0)	28.0	25.06	<0.001
Number of pulses	7.0 ± 2.26 (4–12)	32.2	14.9 ± 7.78 (5–33)	52.3	5.4 ± 3.11 (3–12)	57.9	7.4 ± 1.07 (6–9)	14.5	29.07	<0.001
Mean pulse period (ms)	91.5 ± 20.35 (57.0–119.6)	22.2	86.8 ± 18.46 (60.3–132.6)	21.3	100.4 ± 13.33 (78.7–116.1)	13.3	82.6 ± 20.72 (52.7–134.7)	25.1	6.26	ns
Initial pulse period (ms)	82.7 ± 20.08 (51.0–110.3)	24.3	69.2 ± 21.67 (37.8–124.8)	31.3	90.8 ± 13.35 (70.8–114.3)	14.7	76.9 ± 24.26 (52.6–141.4)	31.6	10.73	0.01
PF 1 (Hz)	132.8 ± 15.26 (117.2–164.1)	11.5	149.5 ± 30.66 (109.4–257.8)	20.5	128.9 ± 17.72 (117.2–164.1)	13.7	140.6 ± 0.00 (140.6–140.6)	0.0	8.52	0.04
PF 2 (Hz)	459.0 ± 52.37 (375.0–539.1)	11.4	488.7 ± 62.07 (398.4–585.9)	12.7	454.1 ± 48.43 (375.0–539.1)	10.7	471.1 ± 30.15 (421.9–492.2)	6.4	1.60	ns

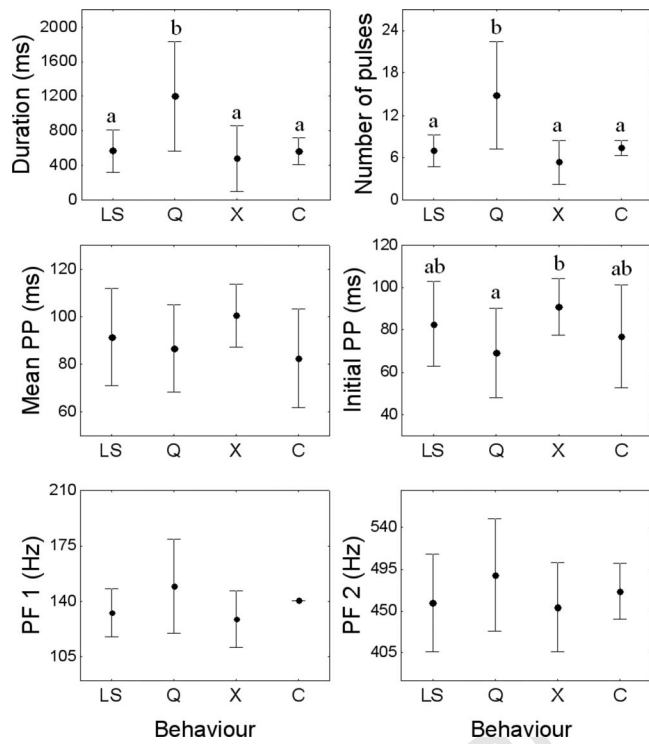


FIG. 3. Variation of courtship sound parameters in *Pseudotropheus zebra* males during lead swim (LS), quiver (Q), sounds produced with no apparent body movement (X), and circle (C). Groups that are significantly different ( $\alpha=0.05$ ) are indicated by different letters (results from Tukey tests). Both “Mean PP” and “Initial PP” refers to mean values of pulse periods; whereas the first is the mean of the pulse periods throughout the entire sound, the second indicates the mean of the first five pulses. Note that comparisons considered data pooled for all males due to the small sample sizes obtained for LS, X, and C. Only a subsample of quiver sounds was considered for the analyses (see methods).

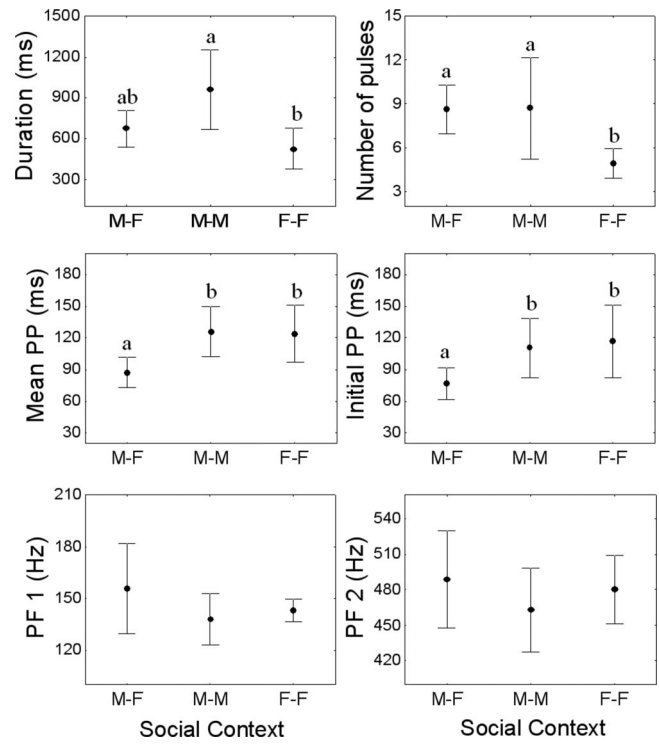


FIG. 4. Variation of the acoustic parameters of quiver sounds emitted in courtship (male–female) and agonistic interactions (male–male and female–female) by *Pseudotropheus zebra*. Groups that are significantly different ( $\alpha=0.05$ ) are indicated by different letters (results from Dunn tests).

280 pale. They sometimes bit at the dominant male’s anal fin  
 281 eggspots, in a similar manner to a female during courtship.  
 282 Commonly, dominant males produced sounds during such  
 283 agonistic quivering. In female–female encounters, sounds  
 284 were generally produced during agonistic quivers, often by  
 285 females that showed sexual readiness or during mouthbrood-  
 286 ing, which also seemed to be more aggressive (three out of  
 287 five females producing recorded sounds were mouthbrood-  
 288 ing).  
 289 Sounds produced in male–female, male–male, and  
 290 female–female encounters differed significantly in all tempo-  
 291 ral parameters but not in the frequency domain (Table I, Figs.  
 292 4 and 5). Male sounds were longer and included more pulses  
 293 than those emitted by females; moreover, male sounds also  
 294 differed in duration according to social context (Fig. 4).  
 295 Courting male sounds also showed significantly shorter initial  
 296 and mean pulse periods than agonistic sounds by either  
 297 sex (Fig. 4).

298 IV. DISCUSSION

299 A. Male courtship sounds

300 The present study has shown that *Pseudotropheus zebra*  
 301 males produce sounds not only in the early stages of court-  
 302 ship, during quiver, but also during courtship displays that  
 303 occur closer to spawning. Moreover, the sound production in

the presence of females but without any other noticeable be- 304  
 havioral display, consistent with observations on another 305  
 Malawian haplochromine cichlid *Tramitichromis interme- 306*  
*dius*, suggests that sound can be a purposely generated uni- 307  
 modal courtship display (Ripley and Lobel, 2004). 308  
 Courtship sounds varied in their characteristics accord- 309

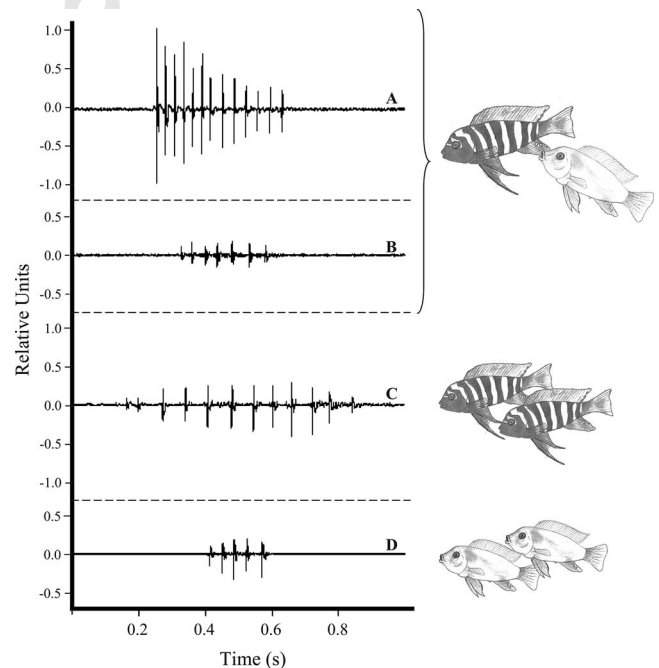


FIG. 5. Oscillograms of sounds produced associated with different contexts and gender: (A) male courtship quiver, (B) circle, (C) male agonistic quiver, and (D) female agonistic quiver. Sampling frequency 48 kHz.

ing to the associated courtship behavior, being longer and with a higher pulse rate during quivering (Fig. 3). Although only a small sample size of late stage courtship sounds was recorded, the present results indicate that acoustic communication is more diversified during the courting activities than previously reported. In other cichlids, sound production seems mostly restricted to male quivering during the early stages of courtship (Ripley and Lobel, 2004, reviewed in Amorim *et al.*, 2004), except in the Mozambique tilapia *Oreochromis mossambicus* that produces sounds throughout courtship (Amorim *et al.*, 2003). In *O. mossambicus*, sounds are longer and with a faster pulse rate during the late courtship behavior of tail wagging (Baerends and Baerends van Roon, 1950) than during other courtship activities (Amorim *et al.*, 2003). Although performed in different phases of courtship, the quivering of *P. zebra* and the tail wagging of *O. mossambicus* are probably equivalent in function. Both consist of displays in which males quiver their bodies vigorously, simultaneously emitting sounds in close proximity of the female, and may convey information of their quality and motivation. In addition, both *P. zebra* and *O. mossambicus* males may quiver and tail wag in all stages of courtship (Baerends and Baerends van Roon, 1950), particularly when females begin to wander out of a male's core spawning area.

Male motivation and quality may be advertised by higher calling rates, longer calls, and higher pulse repetition rates that are likely to be more energetically expensive. At least in some species these parameters may be assessed by females during mate choice. For example, in the gray tree frog *Hyla versicolor*, females prefer longer male calls with a higher pulse number to shorter calls (Gerhardt *et al.*, 2000), and this parameter is an indicator of male genetic quality (Welch *et al.*, 1998). In fishes, Thorson and Fine (2002) demonstrated that males *Opsanus beta* call faster at twilight, shortening and simplifying their multiboop calls, suggesting a tradeoff between call repetition rate and complexity in female choice. In invertebrates, pulse number and rate, together with sound frequency, are the most important acoustic features involved in female choice (e.g., Simmons, 1988).

Other sound parameters may transmit additional information relevant to female mate choice. Quiver sounds differed considerably among individual males, for example with larger males producing lower frequencies at PF2. This parameter was also the one that showed the least intraindividual variation (Table I), probably because it may be dependent on male size (Lobel, 2001; Amorim *et al.*, 2003) rather than motivation. Male size is often regarded as an indication of higher fitness and in cichlids may be related to social status and breeding success (e.g., Oliveira *et al.*, 1996).

The association of courtship quiver sound parameters (PF1 and pulse period) with the number of eggspots in the anal fin is less obviously explicable. Perhaps these parameters are independent indicators of some common cause, such as overall male fitness. Eggspot number was correlated with fish size in other cichlids (Goldschmidt, 1991), although it does not seem the case in *P. zebra* perhaps because of species differences or the restricted size of fish used. Females of several haplochromine cichlids are known to choose mat-

ing partners on the basis of their eggspot number (Coultridge and Alexander, 2001) and in some *Pseudotropheus* species, females prefer a larger number of eggspots (Coultridge and Alexander, 2001). In *P. zebra*, lower sound-peak frequency at PF2 and especially higher pulse rate may indicate better male condition and could be used with additional visual cues from the eggspots in mate sexual selection.

## B. Agonistic sounds

Sound produced by both sexes during agonistic contexts is described in this study for *P. zebra* for the first time and has been documented for a number of cichlid species (reviewed by Lobel, 1998; Amorim, 2006). We found several significant differences in the sounds produced in agonistic context by males and females (Fig. 4). Aggressive males produced significantly longer and more pulsed sounds than females. In addition, male sounds also differed according to the social context. Courtship sounds were shorter and also had a faster pulse repetition rate than male agonistic sounds (Fig. 4). In line with our observations, in the croaking gouramis (*Trichopsis vittata*), where only females produce sounds during mating (Brittinger, 1991; Ladich, 2007), female courtship croaks are also produced at a faster rate than the aggressive croaks produced by both sexes (Brittinger, 1991). Similarly, the intervals between the double pulses that make up a croak also differ between sexes and social context (Brittinger, 1991). Although there are relatively few published quantitative comparisons of the influence of sex and social context on fish sounds, taken together, the results with *T. vittata* and the present study data with *P. zebra* suggest that temporal parameters of fish sounds may contain information on the motivation and gender of the sound producer. Sounds may carry information about male quality or motivation, which may influence the outcome of contests, in a manner similar to that proposed for female mating decisions. Playback of conspecific aggressive sounds may inhibit aggression in *Cichlasoma* (now *Archocentrus*) *centrarchus*, a Central American cichlid fish (Schwarz, 1974), whereas *Trichopsis* males that vocalized during contests had an increased chance of winning (Ladich *et al.*, 1992). In other taxa, a classical example is provided by male toads, *Bufo bufo*, that settle contests for the possession of females by signaling body size and hence fighting ability with call frequency (Davies and Halliday, 1978).

Sound production by female *P. zebra* was noted in a previous study, but not analyzed or compared with sounds made by males (Amorim *et al.*, 2004). Sound was only produced when females appeared to be sexually receptive (when the ovipositor was visible) or mouthbrooding, both situations where females typically become more aggressive. Similarly, sound production by mouthbrooding females has been documented for *O. mossambicus* (Marshall, 1971). In another cichlid fish, *A. centrarchus*, both sexes made sounds during the breeding cycle in an aggressive context (Schwarz, 1980). Females of this substrate spawning species emit sounds mainly during brood defence but also during nest preparation before spawning. It has been suggested that sound production by female fish may be more frequent than previously



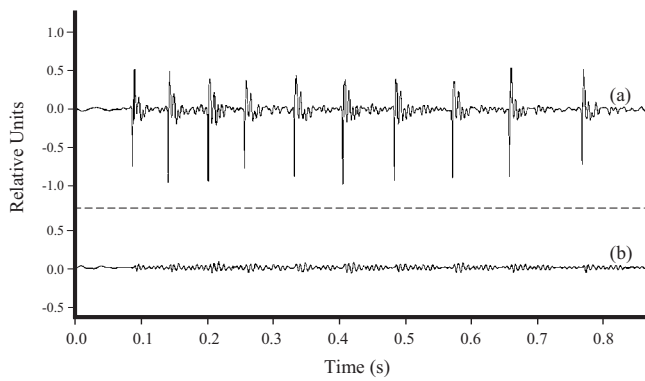


FIG. 6. Oscillograms of a courtship sound produced by a *Pseudotropheus zebra* male recorded at a distance of (a) 5 cm and (b) 40 cm from the hydrophone, in this case, sound attenuation was approximately 20 dB. Sampling frequency 48 kHz.

426 thought, perhaps because the sound producing apparatus is  
427 often less developed than in the male, resulting in weaker  
428 vocalizations, which are harder to detect (Hawkins, 1993;  
429 Ladich, 2007).

### 430 C. Concluding remarks

431 The variation in sounds we have documented indicates  
432 that *P. zebra* vocalizations have the potential to carry infor-  
433 mation about sex, size, motivation, and other fitness param-  
434 eters that may play a role in sexual selection. Although ab-  
435 solute sound pressure levels have yet to be measured, it is  
436 clear that the sounds made by *P. zebra* are of low amplitudes  
437 and attenuate severely within short distances from the sender  
438 (Fig. 6), and it is unlikely that they are used to attract mating  
439 partners or to repel rivals at distance (Krebs *et al.*, 1978).  
440 More probably, and consistent with the behavioral contexts  
441 in which the sounds were observed, acoustic signals may be  
442 important during close-range encounters already initiated on  
443 the basis of visual signals. As females may reject males at  
444 this stage of a courtship sequence, and territorial rival males  
445 may decide to flee or continue fighting, close range sounds  
446 may play a major and complex role in the social behavior of  
447 *P. zebra* and other African cichlid fishes.

448 This study is a detailed description of sounds produced  
449 during courtship and agonistic interactions in the cichlid  
450 *Pseudotropheus zebra* and reveals an acoustic repertoire  
451 richer than previously thought. It emphasizes the need of  
452 additional research to clarify the behavioral functions of the  
453 sounds that may have also played a role in the rapid specia-  
454 tion of African cichlids.

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