

BRIEF COMMUNICATIONS

African cichlid *Pseudotropheus* spp. males moan to females during foreplay

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This study describes a new courtship sound (moan) produced by *Pseudotropheus* spp. males, not previously reported for cichlids. Moans are short tonal sounds often showing frequency modulation. This sound type is of very low amplitude and is produced when males swim in close proximity to a female, usually before performing more exuberant behavioural exhibitions, such as darting, quivering the body and growling.

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Male sexual displays may influence female mating preferences (Anderson, 1994). In African cichlids, male visual, chemical and acoustic signals have been shown or suggested to influence female intra- and interspecific mate choice (Knight & Turner, 1999; Amorim *et al.*, 2004; Plenderleith *et al.*, 2005; Simões *et al.*, 2006). In the Cichlidae, sounds emitted during courtship consist of a series of low frequency pulses, growls, which are usually produced while males are quivering (Amorim, 2006). The present study describes for the first time a very low frequency tonal sound (moan) produced during courtship behaviour by cichlid males (*Pseudotropheus* spp.).

In these experiments multiple recordings were analysed from single males (25 males, 76 moans) during courtship interactions. A total of nine *Pseudotropheus fainzilberi* Staeck, 1976, seven *Pseudotropheus emmiltos* (Stauffer *et al.*, 1997), nine *Pseudotropheus* ‘zebra gold’ (Ribbink *et al.*, 1983) × *Pseudotropheus zebra* (Boulenger, 1899) hybrid adult males were tested. Since the variability in

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moans emitted by individual males and between males of different species was very low, the data were pooled for all species. Experiments were conducted in four tanks (1000 × 500 × 400 mm high), each transversally divided in three compartments by two opaque removable partitions. Tanks were fitted with two internal power filters and maintained at 25–27° C by an internal 250 W heater, on a 12L:12D cycle provided by room lights. Fishes were fed twice daily with a mixture of commercial cichlid flakes and koi *Cyprinus carpio* L. pellets (Astra, Bissendorf, Germany). In the lateral compartments (300 mm wide), males were provided with terracotta pots and left to acclimatize and become territorial for a minimum of 12 h prior to the recordings. The central compartment (400 mm wide) housed five to seven conspecific females. Recording tanks were placed on top of a thick rock-wool layer providing insulation from external noise transmitted through floor vibrations. This setup has proved to be effective in reducing low-frequency noise and considerably increased the signal-to-noise ratio. Before each recording session, all electric appliances (aeration, filters and lights) were switched off. Recordings lasted for 20 min and started by removing one of the partitions allowing the focal male to interact with the females. At the end of each recording session, the focal male was weighed (wet mass, M), measured (standard length, L_S) and returned to a stock tank. Male size averaged 123.3 ± 8.2 (106.0–145.0) mm L_S [mean \pm s.e. (range)] and 65.6 ± 15.8 (41.4–106.9) g M .

Sounds were recorded using two High Tech 94 SSQ hydrophones (Gulfport, MS, U.S.A.) (sensitivity of -165 dB re $1\text{V}\mu\text{Pa}^{-1}$) and a Pioneer DVD Recorder DVR-3100 (Tokyo, Japan) (frequency response within ± 1.5 dB from 40 Hz to 2 kHz, sampled at 48 kHz, 24 bit), and analysed with Adobe Audition 2.0. (Adobe Systems Inc., 2005, San Jose, CA, U.S.A.) and Raven 1.2.1 (Cornell Lab of Ornithology, 2003, Ithaca, NY, U.S.A.). Only sounds that showed a high signal:noise ratio usually recorded at 10–40 mm from the focal fish were considered. The acoustic variables analysed were sound duration (ms), the peak frequency (Hz) and the change in peak frequency observed in frequency modulated moans (Fig. 1). Moans could be discriminated into two types depending on whether or not there was frequency modulation occurring (Fig. 1). Frequency modulation was quantified as the difference between the initial and the final peak frequencies in a moan (M1 and M2) measured in the first harmonic. Temporal features were measured from oscillograms and peak frequencies from power spectra based on 2048 point fast fourier transform (FFT) with a Hamming window applied (Amorim *et al.*, 2004).

Moans had usually very low amplitudes and were only detected when males produced a moan especially close to the hydrophone (less than one body length). Males moaned in very close proximity to the females while displaying their flanks, often before darting and quivering in front of the females (Fig. 2). Frequency-modulated moans ($n = 56$) had a mean duration of 550.4 [\pm s.d. (range) = ± 118.9 (333.6–796.1)] ms, and two parts could be distinguished (M1 and M2; Fig. 1). The first part of the moan (M1) had a peak frequency of 34.4 ± 7.9 (21.5–53.8) Hz. Peak frequency increased at the end of the moan (M2) by 27.2 ± 12.5 (3.9–62.5) Hz on average. Moans with no frequency modulation (Fig. 1; $n = 20$) were similar in terms of duration, 513.5 ± 130.5 (282.1–833.4) ms, and the peak frequency was 44.1 ± 20.3 (23.4–86.1) Hz.

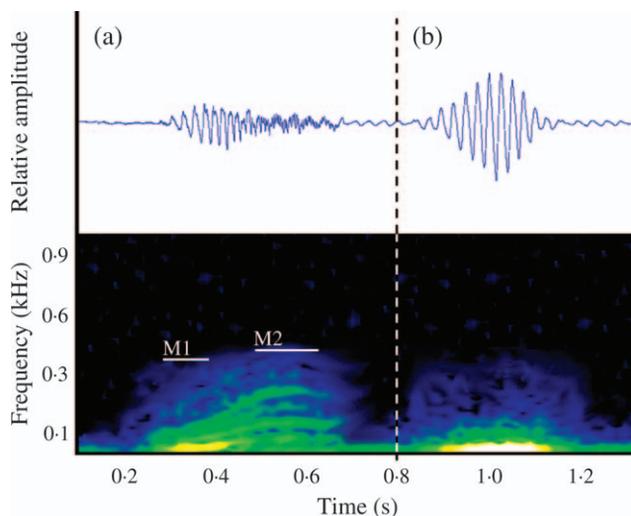


FIG. 1. Oscillogram and sonogram of (a) a modulated and (b) an unmodulated moan sound emitted by *Pseudotropheus* spp. males (*Pseudotropheus emmiltos* in the example). Two parts in which the (a) moan sounds were divided for analysis are indicated in the sonogram: the peak frequency of the first (M1) and second parts (M2) were compared to measure the modulation of the sound.

Usually, moans with frequency modulation also showed amplitude modulation with a reduction in amplitude towards the end of the sound (Fig. 1).

The present study describes, for the first time in the Cichlidae, a tonal sound produced during courtship interactions. In other cichlid species, e.g. *Oreochromis*

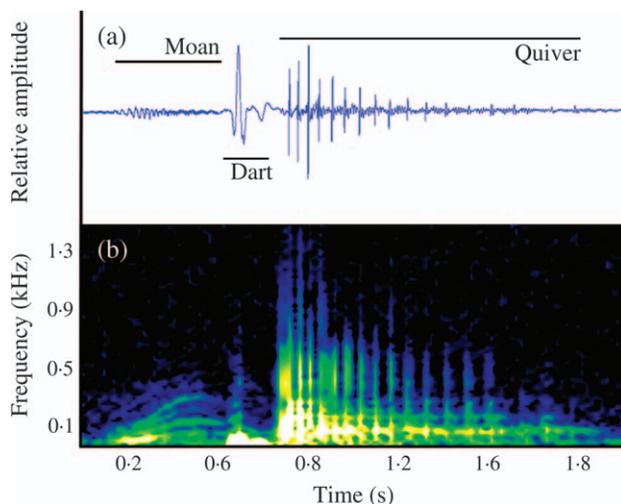


FIG. 2. (a) Oscillogram and (b) sonogram of a moan sound emitted by *Pseudotropheus* spp. males (*Pseudotropheus emmiltos* in the example). Typical dart and quiver sounds are also shown in the sonogram, allowing the comparison between these sounds in terms of frequency and amplitude. Sounds associated with darts are involuntary and result from the exaggerated 180° turns that males perform during this behaviour.

mossambicus (Peters, 1852) (Amorim *et al.*, 2003) and *Cichlasoma centrarchus* (Gill, 1877) (Schwarz, 1974), males are known to produce growling sounds to court females, which were considered as the single cichlid courtship sound type (Amorim, 2006). In some other fish families, males also use tonal sounds during courtship, for instance to attract females to their nests or during spawning (e.g. *Batrachoididae*: Thorson & Fine, 2002; *Mormyridae*: Crawford *et al.*, 1997; *Ostraciidae*: Lobel, 1996; *Gadidae*: Hawkins, 1993). In these cases, males' emitted sounds are produced by very fast contractions of the intrinsic sonic muscles on the swimbladder (Fine *et al.*, 2001). In cichlids, sounds have been suggested to be produced by the pharyngeal apparatus and then amplified by the swimbladder (Lobel, 2001; Rice & Lobel, 2002). Although the previous hypothesis has not yet been demonstrated, this study suggests that maybe a different mechanism could be used to produce these tonal sounds.

Moans are less conspicuous signals than growls and are characterized by their lower amplitude and lower peak frequency (see Fig. 2). Moan sounds had considerably lower peak frequencies than quiver sounds of the same species. Amorim *et al.* (2004) and Amorim *et al.* (2008) concluded that courtship quiver sounds in the same species of the *Pseudotropheus* genus had mean peak frequency of *c.* 430–520 Hz. It is likely that this inconspicuous acoustic signal may serve to draw the attention of the female to the more spectacular displays such as darts and quivers (typically accompanied by growls) that often follow the production of moans.

The weak moaning sounds reported here were probably overlooked before because of their quietness and the lack of acoustic insulation in the recording setup. These tonal sounds may be regarded as 'conspirational whispers', like the majority of courtship signals (Krebs & Dawkins, 1984). Moans are generally produced in very close proximity to females and only when they seem to be receptive to male courtship displays. Fish courtship sounds are typically co-operative signals that benefit both sender and receiver and probably help synchronize gamete release (Ladich, 2007). Such quiet co-operative signals are generally less energetically costly and less likely to attract predators and sexual competitors than louder sounds, characteristic of agonistic contexts (Ladich, 2007).

In this study, two types of moans were identified: one with an increase in frequency in the second part of the sound and another with constant frequency. Usually sounds produced with no variation in frequency had higher amplitude but were similar in terms of duration. Most fishes show poor frequency modulation, have limited acoustical repertoires and relatively few species of fishes produced more than one or two distinct sound types (Amorim, 2006). Nonetheless, some *Pseudotropheus* species seem to have developed a considerable variability in their sounds. In addition to exhibiting two sound types associated with courtship (Amorim *et al.*, 2004; present study), growls vary in some of their acoustic variables depending on the context of sound production (courtship *v.* agonistic) and on the sex of the emitter (Simões *et al.*, 2006). The discovery of this elaborate sonic repertoire enhances the likelihood that scientists will appreciate the importance of acoustic communication for these extremely visual and colourful African cichlid species.

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References

- Amorim, M. C. P. (2006). Diversity of sound production in fish. In *Communication in Fishes* (Ladich, F., Collin, S. P., Moller, P. & Kapoor, B. G., eds), pp. 71–105. Enfield: Science Publishers.
- Amorim, M. C. P., Fonseca, P. J. & Almada, V. C. (2003). Sound production during courtship and spawning of the cichlid *Oreochromis mossambicus*: male–female and male–male interactions. *Journal of Fish Biology* **62**, 658–672. doi: 10.1046/j.0022-1112.2003.00054.x
- Amorim, M. C. P., Knight, M. E., Stratoudakis, Y. & Turner, G. F. (2004). Differences in sounds made by courting males of three closely related Lake Malawi cichlid species. *Journal of Fish Biology* **65**, 1358–1371. doi: 10.1111/j.0022-1112.2004.00535.x
- Amorim, M. C. P., Simões, J. M., Fonseca, P. J. & Turner, G. F. (2008). Species differences in courtship acoustic signals among five Lake Malawi cichlid species (*Pseudotropheus* spp.). *Journal of Fish Biology* **72**, 1355–1368.
- Anderson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Crawford, J. D., Cook, A. P. & Heberlein, A. S. (1997). Bioacoustic behavior of African fishes (Mormyridae): potential cues for species and individual recognition in *Pollimyrus*. *Journal of the Acoustical Society of America* **102**, 1200–1212.
- Fine, M. L., Malloy, K. L., King, C. B., Mitchell, S. L. & Cameron, T. M. (2001). Movement and sound generation by the toadfish swimbladder. *Journal of Comparative Physiology A* **187**, 371–379.
- Hawkins, A. D. (1993). Underwater sound and fish behaviour. In *Hearing and Sound Communication in Fish* (Tavolga, W. N., Popper, A. N. & Fay, R. R., eds), pp. 129–169. New York: Springer-Verlag.
- Knight, M. E. & Turner, G. F. (1999). Reproductive isolation among closely related Lake Malawi cichlids: can males recognise conspecific females by visual cues? *Animal Behaviour* **58**, 761–768.
- Krebs, J. R. & Dawkins, R. (1984). Animal signals: mind reading and manipulation. In *Behavioural Ecology. An Evolutionary Approach*, 2nd edn (Krebs, J. R. & Davies, N. B., eds), pp. 380–402. Oxford: Blackwell Scientific.
- Ladich, F. (2007). Females whisper briefly during sex: context- and sex-specific differences in sounds made by croaking gouramis. *Animal Behaviour* **73**, 379–387.
- Lobel, P. S. (1996). Spawning sound of the trunkfish, *Ostracion meleagris* (Ostraciidae). *The Biological Bulletin* **191**, 308–309.
- Lobel, P. S. (2001). Acoustic behaviour of cichlid fishes. *Journal of Aquaculture and Aquatic Sciences* **9**, 167–186.
- Plenderleith, M., van Oosterhout, C., Robinson, R. L. & Turner, G. F. (2005). Female preference for conspecific males based on olfactory cues in a Lake Malawi cichlid fish. *Biology Letters* **4**, 411–414.
- Ribbink, A. J., Marsh, B. A., Marsh, A. C., Ribbink, A. C. & Sharp, B. J. (1983). A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *South African Journal of Zoology* **18**, 149–310.
- Rice, A. N. & Lobel, P. S. (2002). Enzyme activities of pharyngeal jaw musculature in the cichlid *Tramitichromis intermedius*: implications for sound production in cichlid fishes. *Journal of Experimental Biology* **205**, 3519–3523.
- Schwarz, A. (1974). Sound production and associated behaviour in a cichlid fish, *Cichlasoma centrarchus*. I. Male–male interactions. *Zeitschrift für Tierpsychologie* **35**, 147–156.

- Simões, J. M., Duarte, I., Fonseca, P. J., Turner, G. F. & Amorim, M. C. P. (2006). Acoustic behaviour in Malawian cichlids (*Pseudotropheus* spp., Cichlidae): potential cues for species recognition and intraspecific communication. *Razprave IV razreda SAZU, Advances in Bioacoustics II* **47**, 229–236.
- Stauffer, J. R., Bowers, N. J., Kellog, K. A. & McKaye, K. R. (1997). A revision of the blue-black *Pseudotropheus zebra* (Teleostei, Cichlidae) complex from Lake Malawi, Africa, with a description of a new genus and ten new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **148**, 189–230.
- Thorson, R. F. & Fine, M. L. (2002). Crepuscular changes in emission rate and parameters of the boat whistle advertisement call of the gulf toadfish, *Opsanus beta*. *Environmental Biology of Fishes* **63**, 321–331.