Acoustic diversity in Lake Malawi's rock-dwelling cichlids

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Abstract The cichlids of Lake Malawi are one of the world's most species rich and phenotypically diverse groups of extant vertebrates. The extraordinary variability of this group's color patterns, reproductive behaviors, and trophic morphologies are well documented. More recently, an additional axis of phenotypic diversity has been identified. Lake Malawi cichlids have been shown to use species-specific acoustic communication in both aggressive and reproductive encounters. However, documentation of acoustic signals used by this group is limited to a small number of taxa observed within the confines of the laboratory. This study examines the acoustic signals produced by six species spanning four genera of rock-dwelling cichlids recorded in their natural habitat, the shallow waters surrounding Thumbi West Island, Lake Malawi. Four acoustic parameters were quantified and compared between species: trill dura-

tion, number of pulses per trill, pulse duration, and pulse period. Using these characteristics, sympatric species within the genus *Maylandia* were easily distinguished. Furthermore, a comparison of this data to previously published acoustic data reveals possible geographic dialects within species.

Introduction

The cichlids of Lake Malawi have undergone one of the most extensive and rapid radiations identified to date. Since the formation of the lake basin 2 MYA, well over 800 species of cichlid fish have diverged from a single common ancestor. Most fish in this system can be grouped into one of two major clades: the rock-dwelling cichlids and the sand dwelling cichlids (Albertson et al. 1999). These clades are roughly equal in diversity and intense sexual selection is believed to have played a significant role in generating the extraordinary species richness in both groups (Danley and Kocher 2001; Streelman and Danley 2003). As a result, these fish have become a model system for examining recent and rapid speciation events (Kocher 2004; Genner and Turner 2005).

Within the rock-dwelling cichlids, one of the most likely and conspicuous targets of this intense selective

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pressure is male nuptial color pattern. Male color pattern is highly variable in Lake Malawi cichlids, and, as a result, has been the focus of many theoretical and empirical studies on the evolution and diversification of species (van Oppen et al. 1998; Carleton et al. 2006; Carleton 2009; Kidd et al. 2006). However, additional cues such as olfaction and acoustics have been suggested to play an important role in mate choice (Robinson et al. 1998; Knight and Turner 1999; Amorim et al. 2003; Amorim et al. 2004; Plenderleith et al. 2005; Cole and Stacey 2006; Smith and van Staaden 2009). Furthermore, mate choice experiments revealed that visual cues alone are not sufficient to maintain species boundaries (Blais et al. 2009). Hence, non-visual communication could be of higher importance for the maintenance of species boundaries within this system than currently thought.

Fishes can produce sounds in various ways. Specialized skeletal muscles, filaments, pharyngeal jaws and teeth (see Rice and Lobel 2002, 2004; Amorim 2006 for review) can all be used to make sounds. These sounds are then often amplified through the use of the swimbladder as a resonance body. Still, it is not exactly known how the majority of cichlid fishes produce sounds. Ripley and Lobel (2004) and Rice and Lobel (2004) suggested that the pharyngeal jaw, its attached muscles and the swimbladder play an important role for sound production in the Lake Malawi cichlid *Tramitichromis intermedius*. Lanzing (1974) proposed a similar mechanism for the related species *Oreochromis mossambicus*. Longrie et al. (2009) showed that *O. niloticus* produces sound during a backward movement of the pelvic and pectoral girdles and a forward movement of the second pterygiophore of the anal fin. Still it is not clear which sound production mechanisms apply for the acoustic signalling in the rock-dwelling cichlids of Lake Malawi.

Sounds produced by cichlids appear to act in a variety of social interaction. Variations in acoustic signals may be used for identification of conspecific mates and the identification of male quality (Simões et al. 2008a). Amorim et al. (2004), Longrie et al. (2008) and Simões et al. (2008a) demonstrated that cichlids produce sounds during antagonistic encounters and territorial defense as well in courtship. Likewise, females produce sounds as warning or aggressive signals towards each other (Simões et al. 2008a). Still, courtship appears to be the most

important situation in which acoustic signals are emitted (Simões et al. 2008b). These observations are consistent with the use of acoustic signals in a wide variety of fish systems (see Lobel 1992, and Amorim 2006 for reviews). They also illustrate the potential for these signals to contribute to reproductive isolation.

Recently, interest in cichlid acoustic communication has increased and those few studies performed to date have recorded sounds in captivity (but see Lobel 1998). These studies have shown that species can be differentiated based on acoustic characteristics such as trill duration, number of pulses per trill, pulse period, pulse duration, and interpulse interval (Nelissen 1975, 1977, 1978; Lobel 1998, 2001; Amorim et al. 2004, 2008; Simões et al. 2006, 2008a). This study is the first to directly examine the variation of acoustic traits across several species of rock-dwelling cichlids in a wild population. Here, we analyze four parameters of acoustic signals produced by six closely related, sympatric rock-dwelling cichlids of Lake Malawi. We compare our data with previously published studies on Lake Malawi cichlids, some of which examined populations of the same species from different locations.

Materials and methods

We examined male acoustic diversity of six species spanning four genera of Lake Malawi cichlids: *Cynotilapia afra*, *Labeotropheus fuelleborni*, *Maylandia aurora*, *Maylandia callainos*, *Maylandia zebra*, and *Petrotilapia nigra*. (Debate has surrounded the appropriate genus name for those species belonging to what we refer to here as *Maylandia*. Other authors may refer to this genus as either *Pseudotropheus* or *Metriaclima*). All recordings were made in the shallow water (<5 m) around Thumbi West Island, Malawi (14° 01′27.58″ S 34°49′ 25.55″ E).

Males were observed for 20 min prior to recording to identify breeding caves. Breeding caves were identified through observing the focal male attempting to lead a receptive female to a specific area within the rocky substrate. Previous studies have demonstrated that breeding caves are species-specific and are occupied by a single territorial male (Hert 1989; Danley 2001; Jordan et al. 2010). The hydrophone was suspended in the center of male breeding caves

by wedging the hydrophone wire in the surrounding rocks. Breeding caves were approximately 30 cm× 15 cm×25 cm [length × width × depth (Danley 2001)]. Given the placement of the hydrophone, we assume that all the recorded acoustic data were produced by the focal territorial male during courtship. Visual data necessary to validate this assumption are not available. All acoustic signals generated in this cave were recorded for the subsequent 3.5 h.

Recordings were made using a HTI- 96 MIN hydrophone (sensitivity: −163.9 dB 1v/uPA; frequency response: 2 Hz −30 kHz) and a Shure FP11 amplifier. Sounds were recorded using TDK IEC1 Type 1 cassette tapes with a Sony TCM-DV200DV. Recordings were digitized using Audacity, converted to '.wav'-format and input into RavenPro 1.3 software (Charif 2003). Only those trills with waveforms distinct from background noise were analyzed. Oscillograms, spectrograms (frequency v. time), and power spectra (frequency vs. power) were generated and cross-referenced to measure the following four parameters for all species: trill duration, pulse duration, pulse period, and number of pulses per trill (Amorim et al. 2004) (Fig. 1). Because the distance between the hydrophone and the freely behaving focal males were not controlled, center frequency (geometric mean between a lower and an upper frequency threshold) and amplitude of the pulses were not analyzed.

All statistical analyses were run using R 2.9.0 (The R Foundation for Statistical Computing). All data were log transformed prior to analysis. One-way analysis of variance (ANOVA) was used to test for significance in differences in each of the acoustic components. Turkey's HSD test was used for pair wise comparisons.

Results

We were able to record sounds produced by one focal male of each target species. Given the placement of the hydrophone, it is assumed that the recorded sounds were produced during courtship, however visual confirmation of this assumption is not available. The number of analyzable trills recorded during the 3.5 h observation period varied between species (Table 1): *C. afra* $N=5$, *L. fuelleborni* $N=4$, *M. aurora* $N=14$, *M. callainos* $N=17$, *M. zebra* $N=12$ and *P. nigra* $N=6$. Given the low numbers of recorded trills of *C. afra*, *L. fuelleborni* and *P. nigra,* data collected from these species are presented but were not subjected to statistical analysis.

Sounds produced by the *Maylandia* species showed statistically significant differences in three parameters: trill duration (Fig. 2a; $F_{2,34} = 23.55$, $p< 0.0001$), pulse duration (Fig. 2b, $F_{2,37} = 100.16$, $p< 0.0001$), and pulse period (Fig. 2c, $F_{2, 39} = 92.76$ $p< 0.0001$). Pulses per trill (Fig. 2d; $F_{2, 40} = 2.83$; $p= 0.07$) were not significantly different across the three *Maylandia* species.
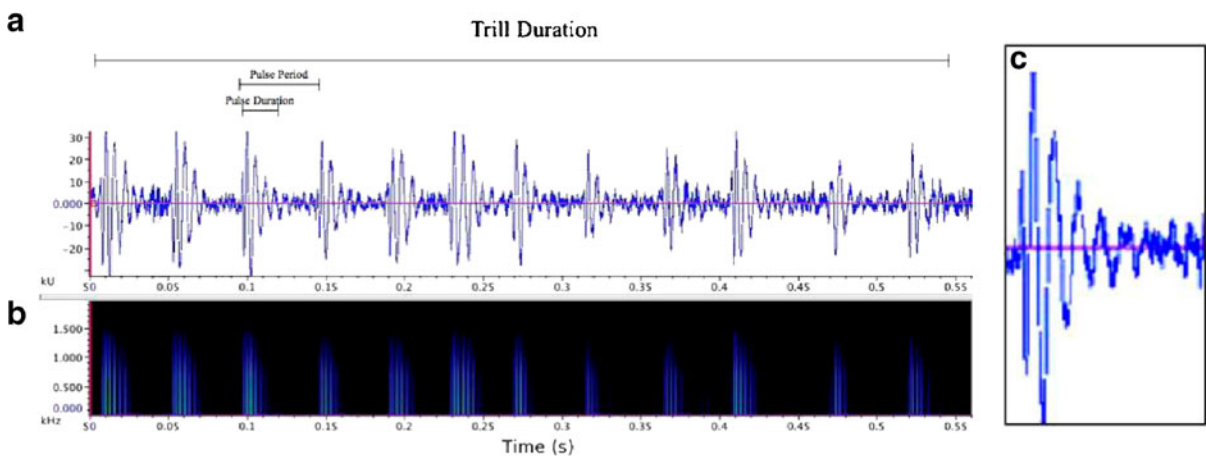

Fig. 1 Typical *M. zebra* trill; trill duration, pulse period, and pulse duration are indicated: **a** Oscillogram (amplitude in kU versus time in seconds), **b** Spectrogram (frequency in kHz versus time in seconds), **c** Detail of a single pulse

Table 1 Means and standard deviations of the acoustic parameters measured in this study

Species	Number of trills analyzed	Trill duration [ms]	Pulses per trill	Pulse duration [ms]	Pulse period [ms]
Cynotilapia afra	5	446.2 +/189.87	13.4 +/− 5.86	9.32 +/− 1.19	34.46 +/− 6.61
Labeotropheus fuelleborni	4	363.75 +/− 148.29	11.5 +/− 3.87	9.23 +/− 0.76	34.73 +/− 5.68
Maylandia aurora	14	375.77 +/− 125.35	11.77 +/− 3.52	12.36 +/− 2.33	34.54 +/− 8.57
Maylandia callainos	17	204.69 +/− 107.67	10.88 +/− 2.88	5.32 +/− 0.99	17.28 +/−4.25
Maylandia zebra	12	763.26 +/− 407.11	17.23 +/− 11.59	16.11 +/− 4.60	55.45 +/− 13.48
Petrotilapia nigra	6	422.33 +/− 217.36	18.33 +/− 8.51	10.0 +/− 3.0	27.92 +/− 4.61

Trill duration of *M. zebra* [763.26 +/− 407.11 ms (mean +/− SD)] was significantly longer than that of *M. aurora* (375.77 +/− 125.35 ms, $p=0.01$) or *M. callainos* (204.69 +/− 107.67 ms, $p<0.001$) (Fig. 2b). *Maylandia aurora* has a significantly longer trill duration than *M. callainos* ($p<0.001$). The remaining species had trill durations of intermediate length: *C. afra* (446.2 +/− 189.87 ms), *L. fuelleborni* (363.75 +/− 148.29 ms) and *P. nigra* (422.33 +/− 217.36 ms).

Pulse duration showed significant differences between all *Maylandia* species (Fig. 2b, $F_{2,37} = 100.16$, $p<0.0001$). Again, *M. zebra* had the longest pulse duration (16.11 +/− 4.60 ms). The pulse duration of *M. callainos* (5.32 +/− 0.99) was shorter than of *M. zebra* ($p<0.001$), while *M. aurora* (12.36 +/− 2.33 ms) had a pulse duration intermediate yet distinct from either *M. zebra* ($p=0.03$) or *M. callainos* ($p<0.001$). Pulse duration of *C. afra* (9.32 +/− 1.19 ms), *L. fuelleborni* (9.23 +/− 0.76 s) and *P. nigra* (10.0 +/− 3.0 ms) had an intermediate length and were most similar to *M. aurora*.

Likewise, all *Maylandia* species could be distinguished based on pulse period (Fig. 2c, $F_{2,39} = 92.758$ $p<0.001$). A pattern similar as for pulse duration was observed; *M. zebra* produced sounds with the longest pulse period (PP = 55.45 +/− 13.48 ms). PP of *M. aurora* was of intermediate length (PP = 34.54 +/− 8.57 ms), whereas *M. callainos* showed the shortest PP (17.28 +/− 4.25 ms). Turkey's HSD test revealed that all pair wise comparisons of *Maylandia* species were significantly different in PP with $p<0.001$. *C. afra* (PP = 34.46 +/− 6.61 ms), *L. fuelleborni* (PP = 34.73 +/− 5.68 ms) and *P. nigra* (PP = 27.92 +/− 4.61 ms) exhibited intermediate pulse periods.

Species could not be distinguished based on the number of pulses per trill (Fig. 2d; $F_{2,40} = 2.83$; $p=0.07$). Admittedly, *M. zebra* (17.23 +/− 11.59)

produced more pulses per trill than *M. callainos* (10.88 +/− 2.88, $p=0.07$), but little difference was observed between *M. aurora* (11.77 +/− 3.52) and *M. zebra* and *M. callainos* ($p=0.21$ and $p=0.86$, respectively). *P. nigra* (18.33 +/−8.51) showed a similar number of trills compared to *M. zebra*; numbers of pulses per trill for *C. afra* (13.4 +/− 5.86) and *L. fuelleborni* (11.5 +/− 3.87) were more similar to *M. aurora*.

Discussion

Recently, the importance of non-visual modalities in the cichlid mate choice has gained recognition. Acoustics and olfaction have been identified as the most important non-visual communication modes in cichlids (Amorim et al. 2004; Almeida et al. 2005; Amorim et al. 2008; Blais et al. 2009). Chemical cues are used in a wide array of social interactions, including the indication of social status (Barata et al. 2007; Bender et al. 2008), reproductive status of females (Clement et al. 2004; Almeida et al. 2005; Miranda et al. 2005) and agonistic interactions (Giaquinto and Volpato 1997). Furthermore, olfactory cues appear to influence female cichlid mate choice (Plenderleith et al. 2005; but see Venesky et al. 2005, and Jordan et al. 2003 for alternative views). Likewise, acoustic communication has been documented as a part of a variety of social interactions

Fig. 2 Histograms of the acoustic characteristics of six mbuna species. The mean and two standard deviations (*bars*) are presented for each species. *Maylandia* species are presented in *black*. Significant differences between species are indicated by bars over the respective species, significance values are *: $p<0.05$, **: $p<0.01$. ***: $p<0.001$ after correction for multiple comparison: **a** Trill duration, **b** Pulse duration, **c** Pulse period, **d** Number of pulses per trill
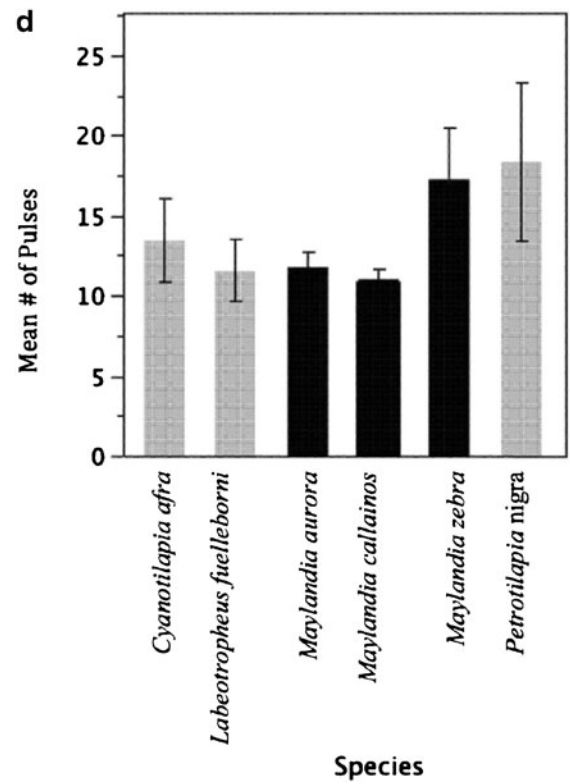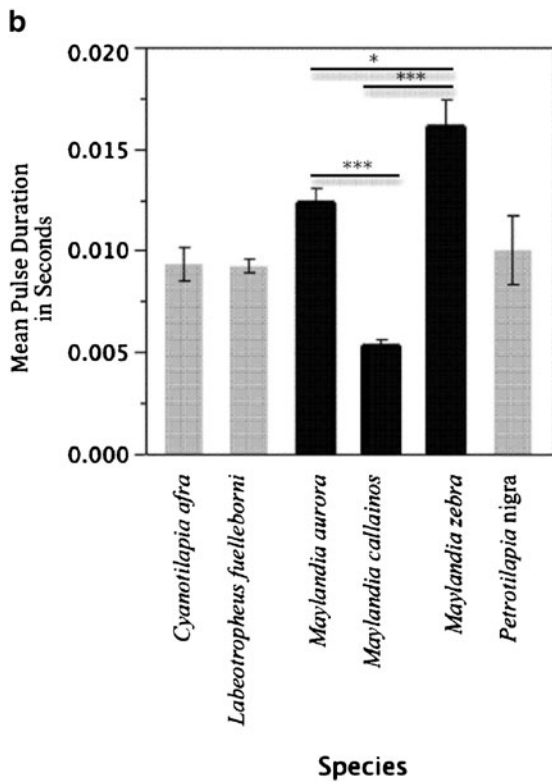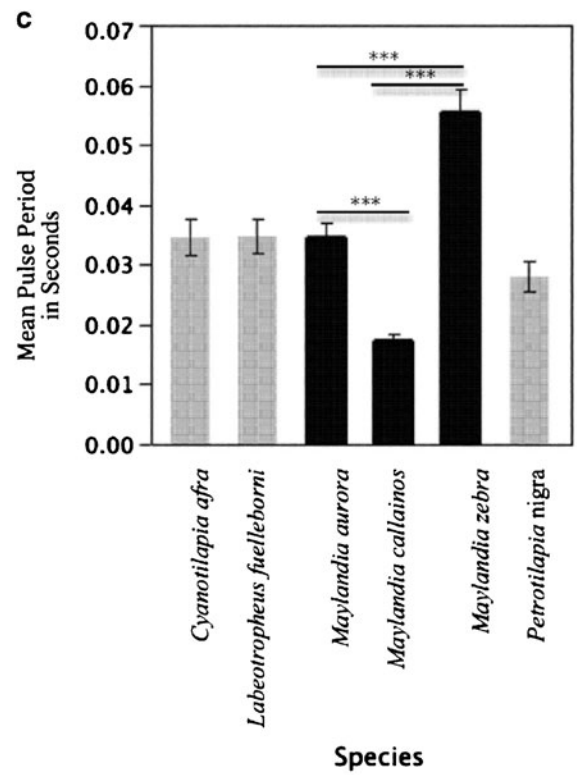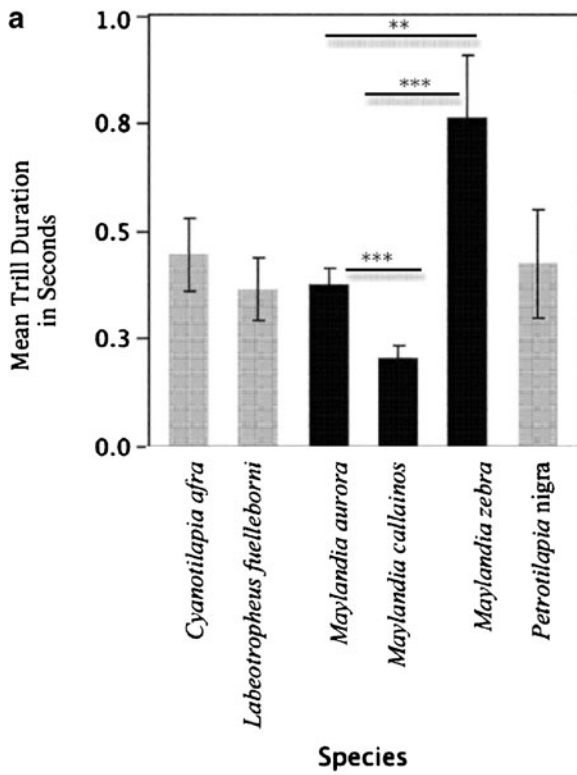
including antagonistic and courtship behavior. Previous studies have shown that species can be differentiated based on acoustic characteristics such as trill duration, number of pulses per trill, pulse period, pulse duration, and interpulse interval (Nelissen 1975, 1977, 1978; Lobel 1998, 2001; Amorim et al. 2004; Simões et al. 2006; Amorim et al. 2008; Simões et al. 2008a).

Our data are consistent with the hypothesis that sympatric species vary in their acoustic signals and that these signals may play a role in mate choice among the cichlid fishes of Lake Malawi. While temporal discrimination of these fish has not been specifically analyzed, studies of other hearing generalists suggest that cichlids are capable of detecting the species specific differences in acoustic behavior documented in these species (reviewed in Amorim et al. 2004). The data presented here indicate that *Maylandia*, if capable of detecting the species-specific temporal differences described here, may use acoustic signals to distinguish con- from heterospecific males. Our data suggest that the three investigated *Maylandia* species can be distinguished based on one or more acoustic parameters. Of the three *Maylandia* species examined, *M. zebra* shows the most distinct sound pattern. *Maylandia zebra* has the longest trill duration, longest pulse duration, and longest pulse period relative to any of the examined species.

A comparison of our dataset to previously published data suggests that acoustic variation exists not only between different species, but also between populations within species (Table 2). The sounds produced by two of the six species examined in this study have been examined in the lab. Four datasets from two locations are available for *M. zebra* [3 Nkhata Bay (Amorim et al. 2004, 2008; Simões et al. 2008a), 1 Thumbi West (present study), and four data sets from two locations for *M. callainos* 3 Nkhata Bay (Amorim et al. 2004, 2008; Smith 2007) 1 Thumbi West (present study)].

While a statistical comparison of the data was not possible due to the different ways of describing variation given in the publications, we can identify substantial differences in analyzed parameters within and between species. Within *M. callainos*, trill duration, pulse period, and pulse duration are distinctly shorter in the Thumbi West population compared to Nkhata Bay. The number of pulses per trill

Table 2 Previously published data on the acoustic characteristics of *M. callainos* and *M. zebra*

Species	Collection location	Laboratory (L) or field (F) recording	N and sex	Duration [ms]	Number of pulse	Mean pulse period [ms]	Pulse duration	Reference
M. callainos	Nkhata Bay	L	8 M	476.3 (349.4–652.3)	8.0 (5.7–11.4)	66.8 (50.1–78.9)	11.5 (9.6–13.4)	Amorim et al. 2004 mean (range)
M.callainos	Nkhata Bay	L	5 M	659.5 +/− 409.4	8.79 +/− 4.86	n.a.	n.a.	Smith 2007 mean +/− SD
M. callainos	Nkhata Bay	L	13 M	617.7 (349.4–1032.7)	9.5 (6.4–14.7)	72.5 8 (60.6–83.4)	n.a.	Amorim et al. 2008 mean (range)
M. callainos	Thumbi West Island	F	1 M	204.69 +/− 107.67 ms	10.88 +/− 1.63	17.28 +/−4.25 ms	5.32 +/− 0.99 ms	This study mean +/− SD
M. zebra	Nkhata Bay	L	6 M	532.0 (383.5–785.5)	9.1 (7.0–14.1)	65.6 (60.4–74.2)	9.7 (7.5–11.4)	Amorim et al. 2004 mean (range)
M. zebra	Nkhata Bay	L	12 M	671.7 +/− 135.59 (421.4–856.8)	8.6 +/− 1.67 (6.6–12.4)	86.8 +/− 14.37 (67.5–113.3)	n.a.	Simões et al. 2008a mean +/− SD (range)
M. zebra	Nkhata Bay	L	12 M	671.7 (421.4–856.8)	8.6 (6.6–12.4)	86.8 (67.5–113.3)	n.a.	Amorim et al. 2008 mean (range)
M. zebra	Thumbi West Island	F	1 M	763.26 +/− 407.11 ms	17.23 +/− 1.86	55.45 +/− 13.48 ms	16.11 +/− 4.60 ms	This study mean +/− SD

differs less among different populations, but appears to be slightly higher for the Thumbi West population (Table 2). *Maylandia zebra* from Thumbi West produce a greater number of pulses per trill, longer pulse duration and a shorter pulse period than observed for specimens from Nkhata Bay (Table 2).

The comparison of published data in the laboratory and wild population data points toward two interesting observations. First, sympatric species differ in at least one of the observed parameters. Second, populations of the same species at different locations appear to differ in their acoustic patterns. Hence, our data corroborates the conclusions of previously published studies which suggested that (1) acoustic signals may play a role in mate choice and recognition and (2) acoustic signals are diverging between geographically isolated populations. The presence of geographically differentiated dialects may contribute to the reproductive isolation of populations and hence contribute to the high rate of speciation observed in this system. More work is needed to understand population level variation in acoustic signals of Lake Malawi cichlids.

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