Possible species specific courtship sounds by two sympatric cichlid fishes in Lake Malawi, Africa

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Possible species specific courtship sounds by two sympatric cichlid fishes in Lake Malawi, Africa

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Synopsis

Sounds were produced by the males of two species of cichlid fishes while courting females. Each courtship sound consisted of a series of distinct pulses occurring in rapid succession. Courtship sounds produced by *Tramitichromis* cf. *intermedius* and *Copadichromis conophorus* were significantly different in pulse rate and individual pulse durations. For *C. conophorus* calls (n = 127) the mean ± sd number of pulses per call was 10 ± 3 and call duration was 181 ± 59 ms. There was a significant positive linear relationship between call duration and the number of pulses ($r^2 = 0.912$, $p < 0.001$). The dominant frequency of the pulses in calls was 471 ± 50 (range 372–594) Hz (n = 40 calls). *T.* cf. *intermedius* also produced a pulsed courtship call; data (mean + sd) from two male *T.* cf. *intermedius:* 9 ± 2 pulses per call and duration 199 ± 44 ms (n = 20 calls). The linear regression between call duration and number of pulses was positive ($r^2 = 0.463$, $p = 0.001$). Pulse rate within calls of *T.* cf. *intermedius* compared to *C. conophorus* were significantly different ($p = 0.018$). Individual pulse durations were also significantly different ($p = 0.043$) between species. However, interpulse intervals were not significantly different ($p = 0.177$). These cichlids produced courtship sounds that were distinct by individual pulse durations and by pulse repition rate in a call.

Introduction

The cichlids of Lake Malawi form a closely-related species flock of more than 500 endemic species (Fryer & Iles 1972). These fishes differ greatly in their behavior and ecology, moderately in their external morphology and very little in their molecular characteristics (Klein et al. 1993). Mate choice behavior as a mechanism for maintaining species isolation is a central feature of hypotheses explaining cichlid evolution (Dominey 1984, Ribbink 1986, McKaye 1991, Stauffer et al. 1995). Courtship differences among related sympatric species may have been selected for as hybrid offspring would presum-

ably have reduced fitness (Uzendoski & Verrell 1993). The role of mating behavior differences acting as a species isolating mechanism has been widely recognized in many animals (Ayala 1991).

Sound production is, perhaps, the most poorly understood aspect of cichlid courtship behavior. Only 9 of the 936 publications cited in Keenleyside (1991) refer to cichlids producing sounds (see also Nelissen 1991). Even so, it has long been thought that sounds may be important as a means of species recognition and mate location in cichlid fishes (Fryer & Iles 1972). One reason why cichlid bioacoustics has been neglected until now is that the sounds of cichlids and many other species of fishes

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cannot be easily detected by human hearing underwater and, therefore, have gone unnoticed (Lobel 1992, personal observations).

I conducted this field study in Lake Malawi to determine if specific sound patterns were associated with the courtship or mating behavior of the sympatric haplochromine cichlids: *Copadichromis conophorus* Stuaffer, LovVullo & McKaye, 1993 [syn. *C. eucinostpomus* (Regan, 1922)] and *Tramitichromis* cf. *intermedius* (Trewavas, 1931). The reproductive behavior of these fishes, particularly of *C. conophorus*, has been extensively studied (McKaye 1983, 1991, McKaye et al. 1990, Lewis et al. 1986). However, sound production has not been previously reported for either species. In this study, I compared the courtship/mating sounds produced by these two sympatric cichlids to determine whether quantitative differences in their calls could be identified.

Methods

Synchronous audio-video recordings were made underwater using a Sony V-9 eight mm video camera coupled with a hydrophone. The hydrophone had a frequency range of 10 to 3000 Hz and a sensitivity at 10 psi of -162 dBv/μPa $\pm$ 2.0 dB (BioAcoustics Inc., Box 549, Woods Hole, MA 02543). Acoustic analysis was performed using the software SIGNAL (Engineering Design, Belmont, MA 02178) and CANARY (Cornell University, Ithaca, NY). Additional details are given in Lobel & Mann (1995).

Audio-video recordings were made of fishes living directly offshore (depth 3 to 8 m) of Lake Malawi National Park at the site of Golden Sands Campground and the adjacent World Wildlife Federation Education Center, Cape Maclear, Malawi, Africa. Because the site was located inside a national park, collection of specimens was not permitted. Instead, close-up underwater photographs were taken and species identification determined by comparison of my photographs with descriptions in Eccles & Trewavas (1989) and Konings (1990, 1995) and by advice from I. Kornfield and J. Stauffer (personal communication). *Copadichromis conophorus* was

previously recognized as *C. eucinostomus* by many authors (Stauffer et al. 1993). J. Stauffer (personal communication) also notes that *Tramitichromis* is under revision and that the species *T.* cf. *intermedius* located at Cape Maclear will likely be reclassified.

The fishes studied were primarily sand dwelling species that construct a characteristic sand mound which functions as their breeding arena. These sand mounds have been named a 'bower' in analogy to bower birds (McKaye et al. 1990). However, the use of the term 'bower' in this case is not appropriate and the word 'nest' is best used to describe the cichlid sand structures (Tweddle et al. 1998). These nests are used for courting and spawning but not brooding or rearing of offspring (McKaye et al. 1990, Tweddle et al. 1998). The process of nest construction and the mating behavior of these fishes, especially *Copadichromis conophorus*, has been described (McKaye 1983, 1984, 1991, McKaye et al. 1990, Stauffer et al. 1995, Stauffer & Kellogg 1996). Briefly, the male builds the nest by gathering mouthfuls of sand and depositing the load on the mound. When a female approaches a male in his nest, he actively and vigorously responds by spreading his fins and swimming in circular paths around the female leading her into the central area of the depression located on top of the sand mound (nest). The male poses in a lateral display, fins extended, and with a body quiver simultaneous with sound production. The female enters the nest, deposits eggs and then immediately sucks the eggs into her mouth, where they are inseminated (McKaye 1984). Afterwards, the female swims away with the brood. Males do not participate in parental care (McKaye 1983, 1984).

The nests of specific males were identified and recordings made by situating the hydrophone along the rim of a fish's nest with the camera set about 2–3 m away. Once arranged, the camera-hydrophone was activated and left to run autonomously (no diver to cause disturbances) for 30–45 minutes. Five recording sessions were made of 5 different male *Copadichromus conophorus* and four recording sessions of 2 different male *Tramitichromis* cf. *intermedius*. All recordings were in open sand flat areas.

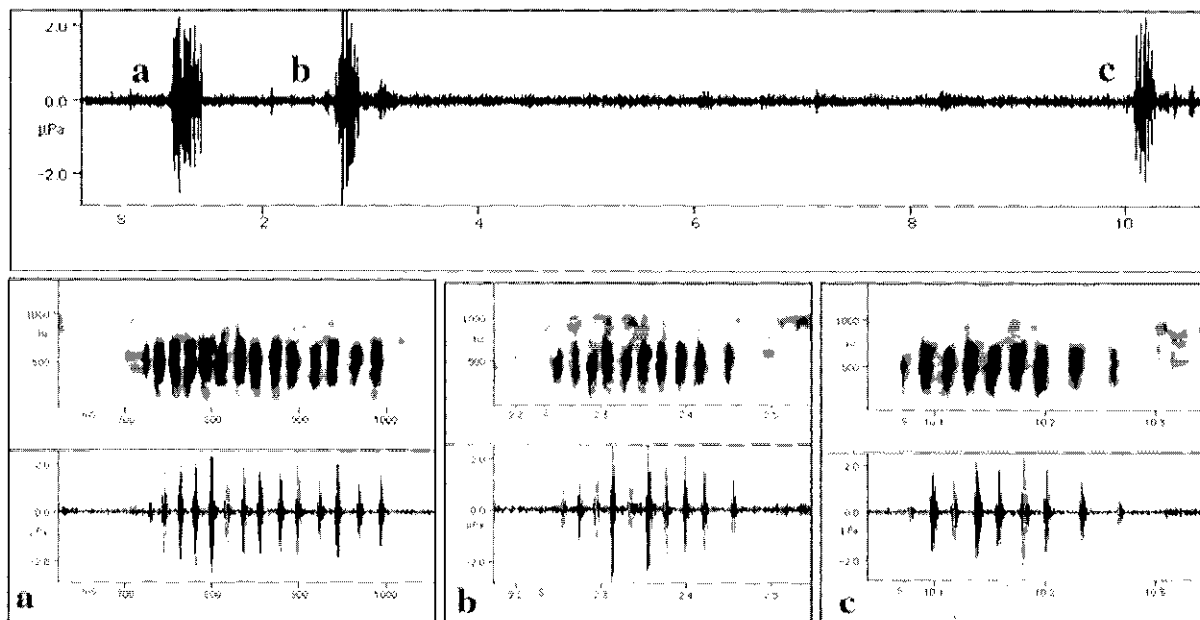In the rock boulder habitat at Otter Point, male

Figure 1. A series of courtship calls produced by a male *Copadichromis conophorus* displaying toward a conspecific female. Top panel is oscillogram showing entire acoustic sequence. Other panels show details of individual calls with a sonogram (top) and oscillogram (bottom): a- male courts as female approaches, 14 pulses, 272.1 ms; b- female enters nest as male circles, 10 pulses, 210 ms; c- female begins to exit nest after mating, male responds by making sound with fins spread, body quivers and zig-zag swimming, 9 pulses, 196.2 ms. The dominant frequency of this male was 517 Hz.

C. conophorus occurred in greater densities than conspecifics in the adjacent open sand habitat. Here, the hydrophone was placed between nests near 3 or 4 males. Five recording sessions were made at five sites. *T.* cf. *intermedius* was not present on top of the rock boulders but was found in the adjacent sand area.

Recordings of *C. conophorus* were made from two groups: one at Otter Point and another in an open sandy area. Since I obtained the most data consisting of several calls from each of several males in from the Otter Point group, I used only this data set in the following analysis. The statistics below are most robust when based upon a data set consisting of multiple recordings from each of several males so that individual variability in sound pattern production is incorporated in the analysis.

Pulse rate is defined as the call duration divided by the number of pulses which gives: ms per pulse. Because of the difficulty of acquiring acoustic data on fishes in the wild, the sample sizes for the number of calls from each species are unequal. Also, the sample size of *T.* cf. *intermedius* calls (N = 20) is

small compared to the number of samples of *C. conophorus* calls (N = 127). This precludes the use of a standard analysis of variance (e.g., Dunn & Clark 1987) and requires instead a nested design. The statistical significance of the difference in the ratio of call duration to the number of pulses between the two species was assessed using the following randomization test (Manley 1991). Suppose that m call sequences are recorded for Group 1 and n call sequences are recorded for Group 2. Under the null hypothesis of no difference between the groups, all possible partitions of the overall set of m+n call sequences into subsets of size m and n are equally likely. There are $(M+n)!/(M!n!)$ such partitions. For each of these, the difference in mean duration: pulse ratio can be calculated. The significance of the observed difference can then be assessed by comparing it to the distribution of differences over the set of partitions. An advantage of this randomization test is that, by randomizing the entire call sequences, it takes any serial dependence in the data into account.

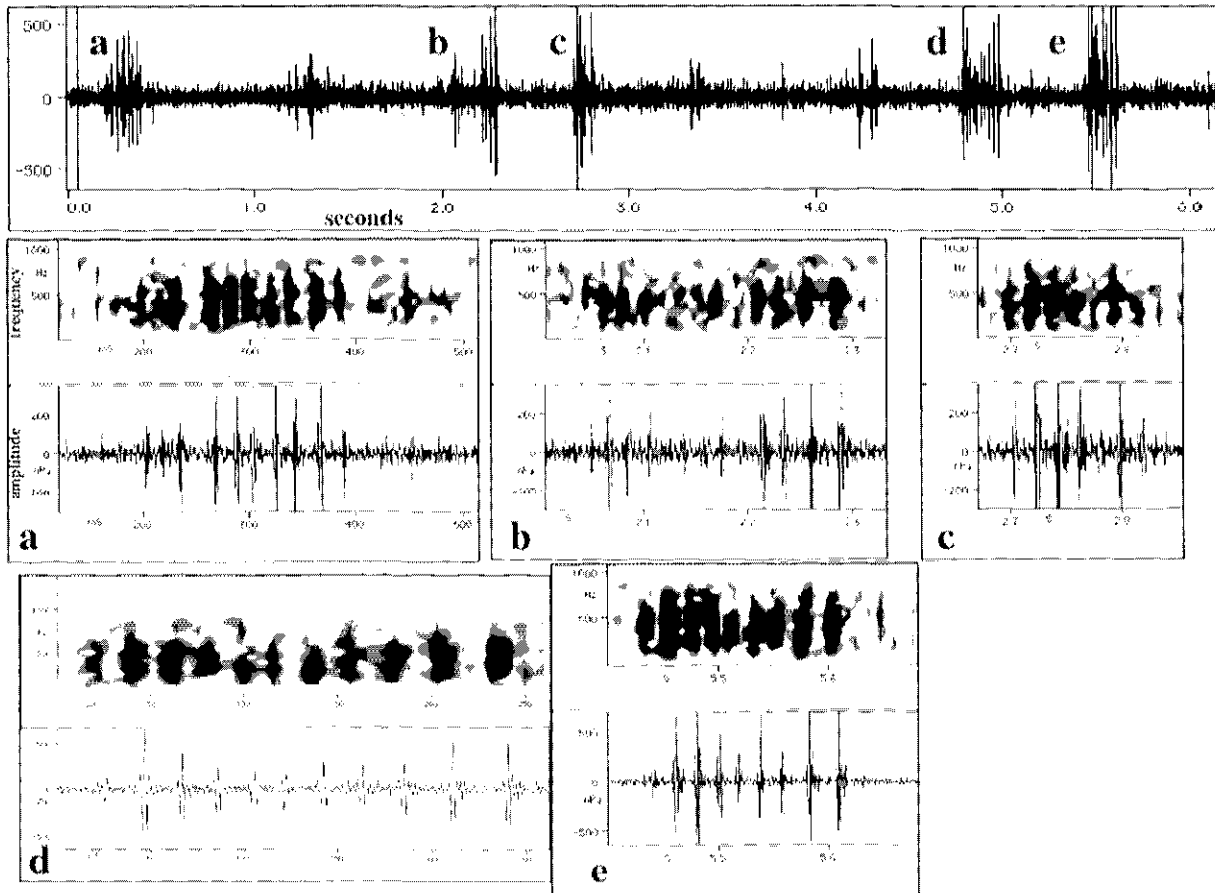Measurements were also made of two other

Figure 2. A series of courtship calls produced by a male *Tramitichromis* cf. *intermedius* displaying toward a conspecific female as she passes by his nest but does not stop to mate. Top panel is oscillograph of the entire acoustic sequence. Other panels show details of each corresponding labeled calls with a sonogram (top) and oscillogram (bottom). The number of pulses per call and call duration were: a- 9 pulses, 195.0 ms; b- 11 pulses, 252.2 ms; c- 7 pulses, 122.7 ms; d- 11 pulses, 231.5 ms; e- 9 pulses, 189.9 ms. The dominant frequency of this male was 345 Hz.

quantitative features of the cichlid sounds: pulse width and the interpulse interval. All measurements were taken using the time-amplitude (oscillographic) sonic analysis. Interpulse interval is the blank space between pulses as defined by relative amplitude of the signal. Pulse width is the time from the start to finish of the signal as defined by the amplitude. Background environmental noises and electrical interference can obscure the precise lines of demarcation between the onset and completion of a pulse signal. For this analysis only the clearest sound recordings were used so that the most precise measurements of interval and pulse durations could be made. Thus, not every pulse or interval of every call was used.

A two-sample separate variance t-test (Systat 7.0) was applied to test the null hypothesis of no difference between the interpulse interval durations and pulse durations for the two species. This statistical test does not require equal variances or samples sizes (SYSTAT software).

Results

Male *Copadichromis conophorus* and *Tramitichromis* cf. *intermedius* produced a distinct sound while displaying courtship behavior toward a conspecific female as she approached and entered the nest. In general, upon a female's approach, the male

swam above the nest and toward the female and produced one or two strong and distinct sound bursts. Sound production was simultaneous with fin fluttering and body quivering. If the female continued her approach into the nest, the male descended to the substrate spawning site, quivered against it and often produced another sound burst. Mating then occurred in quick circular sweeps (see McKaye 1983). A male sometimes produced additional sound bursts in-between spawning bouts when the female was present within the nest. The sounds made by one male *C. conophorus* while courting and mating are shown in Figure 1. The sounds made by one male *T.* cf. *intermedius* courting a female who did not enter the nest or mate are shown in Figure 2.

Although I can not be absolutely certain, it was my impression from having observed these fishes in the field and careful review of the video-acoustic recordings that it was the male producing sounds during courtship in these two species. This assessment is based upon many observations of cichlid and pomacentrid courtship and mating and that sound production is usually accompanied by a body quiver or jerky to exaggerated swimming motions. My impression is also based upon study of the videos and my interpretation of the relative intensity of sound when the male in his nest courted a female as she approached from a few meters away. If the female was producing the courtship call, the sound intensity would have increased as she approached the male next to the hydrophone.

Sound was always associated with courtship behavior. The films made of *C. conophorus* at Otter Point contained 127 calls during 62 male-female encounters made by about 20 males. Forty-two of these calls were identified as produced by 10 males. In these cases the sound was clearly due to a particular individual but when more than one male was actively courting, I could not be certain as to which male produced a call. This data set also includes 22 male-male aggressive encounters and these too were associated with sounds. The films of *C. conophorus* in the sand habitat, where the male bowers were spaced 1–2 meters apart, contain 8 calls made by 6 courting males. There was slight variation in the colors of *Copadichromis conophorus* as shown
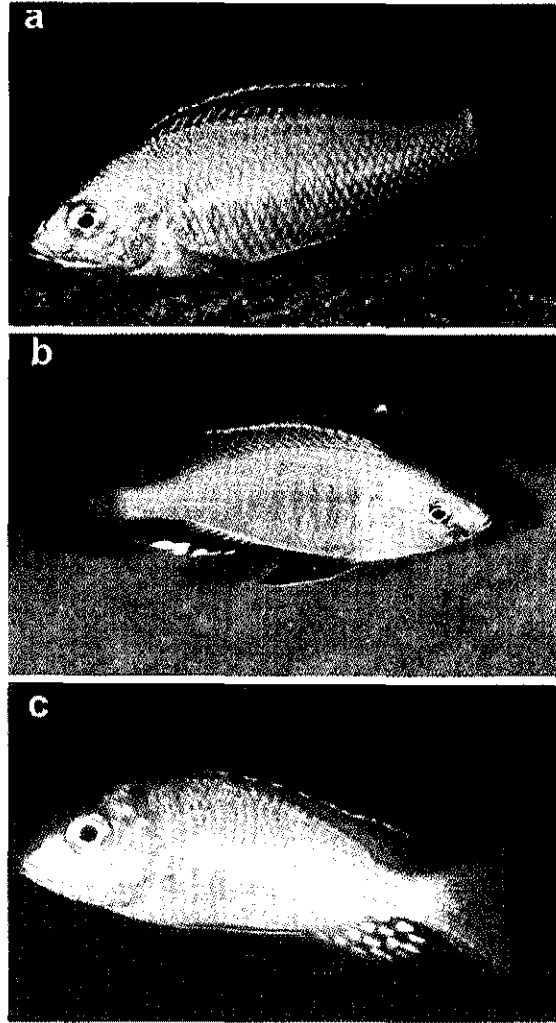

Figure 3. Underwater photographs of male fish. a- *Copadichromis conophorus* on the rock boulder habitat at Otter Point; b- *C. conophorus* in open sand habitat; c- *Tramitichromis* cf. *intermedius* in open sand habitat.

in Figures 3a, b. The films of *T.* cf. *intermedius* (Figure 3c), also in the sand habitat, contain 20 calls made by 2 males during 6 episodes of courtship.

The courtship call pulse patterns of *C. conophorus* are summarized in Table 1. There was a significant positive linear relationship between call duration and the number of pulses ($r^2 = 0.912$, $p < 0.001$, Figure 4a). The mean dominant frequency of pulses measured in 40 calls was 471 Hz $\pm$ 50 SD (range 372–594).

Tramitichromis cf. *intermedius* produces a courtship call that is similar to *C. conophorus* in that both

are composed of a rapid series of pulses. The call pulse patterns from two male *T.* cf. *intermedius* are summarized in Table 2. The linear regression between call duration and number of pulses was positive ($r^2 = 0.463$, $p = 0.001$, Figure 4b). The mean dominant frequency of this species was 388 Hz (range 305–480).

There was no statistical difference (two-sample separate variance t test at 95% CI) between the two species in the number of pulses per call ($p = 0.093$) or in call duration ($p = 0.112$).

The pulse rate is defined as the ratio of call duration divided by the number of pulses within that call. The pulse rate was significantly different between *T.* cf. *intermedius* and *C. conophorus* (Otter Point stock) according to the result of the randomization test (observed differences = 3.51, number of partitions = 55, and $p = 0.018$). Testing the same hypothesis using the separate variance t test corroborated the result that pulse rate was significantly different between the two species ($p < 0.001$).

Pulse duration, ms, was measured from individual pulses within calls. Comparing pulse durations of *C. conophorus* and *T.* cf. *intermedius* suggests that there was a statistically significant species difference (separate variance t test, $p = 0.043$, $n = 62$ pulses from *C. conophorus* and $n = 105$ pulses from *T.* cf. *intermedius*).

The interpulse interval is the period of no sound

Table 1. *Copadichromus conophorus*: descriptive statistics of the courtship call.

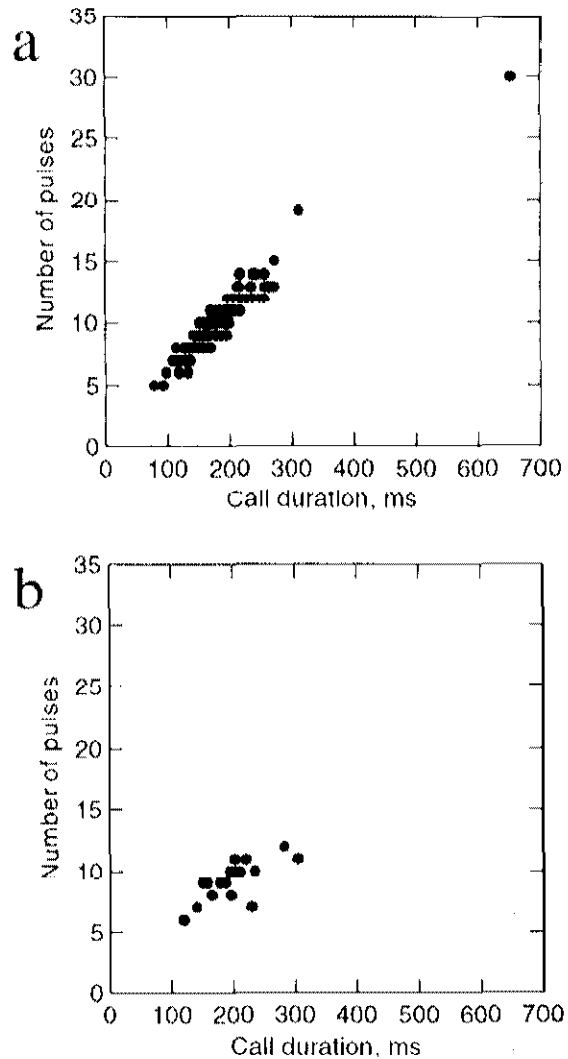|	Call-duration, ms	Number of pulses per call	Duration/number pulse ratio	Interpulse interval, ms	Pulse width, ms
n	127	127	127	56.0	62.0
mean	181.0	10.0	18.0	16.1	6.67
median	171.0	10.0	17.8	14.5	6.30
range	576.0	25	8.0	26.8	7.20
minimum	78.0	5	14.4	8.1	2.70
maximum	654.0	30	22.3	34.9	9.90
variance	3506.8	7.9	2.7	40.5	2.38
SD	59.2	2.8	1.6	6.4	1.54
SE	5.3	0.2	0.1	0.9	0.20
skewness (G1)	4.2	3.1	0.5	1.3	0.34
kurtosis (G2)	30.3	18.9	−0.3	1.3	−0.02
CV%	0.3	0.3	0.1	0.4	0.23

Figure 4. Plots of call duration versus number of pulses for a- *Copadichromis conophorus* on the rock boulder habitat at Otter Point, b- *Tramitichromis* cf. *intermedius* in open sand habitat.

between pulses within a call. There was no statistically significant species difference (separate variance t test, $p = 0.177$, $n = 56$ from *C. conophorus* and $n = 93$ from *T.* cf. *intermedius*).

These results indicate that the pulsed courtship sound patterns produced by *C. conophorus* and *T.* cf. *intermedius* were different in pulse rate and individual pulse durations. There was no difference between species in interpulse interval, number of pulses per call or in call duration.

Table 2. Tramitichromis cf. *intermedius:* descriptive statistics of the courtship call.

	Call-duration, ms	Number of pulses per call	Duration/ number pulse ratio	Interpulse interval, ms	Pulse width, ms
n	20	20	20	93.0	105.0
mean	199.2	9.3	21.5	14.7	6.2
median	199.0	9.5	20.4	13.6	6.3
range	184.0	6	16	26.2	7.8
minimum	120.0	6	16.9	8.1	3.1
maximum	304.0	12	32.9	34.3	10.9
variance	1916.9	2.5	14.1	22.4	1.39
SD	43.8	1.6	3.8	4.7	1.18
SE	9.8	0.4	0.8	0.5	0.12
skewness (G1)	0.6	−0.3	1.5	1.6	0.78
kurtosis (G2)	0.6	−0.7	2.3	3.1	2.72
CV%	0.2	0.2	0.2	0.3	0.2

Discussion

Acoustic differences between the courtship sounds produced by *C. conophorus* and *T.* cf. *intermedius* were found in the most basic temporal elements of the signal. This analysis does not prove that individuals perceive these differences nor that they necessarily use sounds to identify conspecifics as potential mates. However, it does demonstrate that the possibility for acoustic communication exists and is worth further study. The results provide evidence for acoustic cues in *C. conophorus* and *T.* cf. *intermedius* which the females could use in the mate selection process. It was my impression that during this study only the male *C. conophorus* and *T.* cf. *intermedius* produced courtship calls. The dominant frequencies of courtship sounds recorded in this study are within the frequency range of cichlids' hearing (Tavolga 1971, Fay & Popper 1975, Yan & Popper 1992). Interestingly, *T.* cf. *intermedius* and related species possess large sensory pores in the lower jaw which are appearently linked to the lateral line system and presumably function for enhanced sound detection (Konings 1995). It has been speculated that this enlarged sensory pore morphology is an predatory adaptation for specialized hearing of aquatic invertebrate prey burrowing in sand (Konings 1995).

Sonic behavior has been previously described in 16 cichlid species in aquaria (Table 3). However, aquarium recordings can be misleading when interpreting acoustic details of fish sounds because of re-

Table 3. Cichlid bioacoustic studies.

Cichlid	Courtship sound	Aggression sound	Sound producer		Reference
			male	female	
Aequidens portalegrensis		x	not known		Brown & Marshall 1978
Cichlasoma centrarchus		x	x	x	Schwarz 1974a,b,1980
Cichlasoma nigrofasciatum		x		x	Myrberg et al. 1965
Haplochromis burtoni	x	x	x	x	Hirata & Fernald 1975 Nelissen 1977,1978
Hemichromis bimaculatus	x	x	x	x	Myrberg et al. 1965, Rowland 1978
Heterotilapia multispinosa	x	x	x	x	Brown & Marshall 1978
Pterophyllum sp.		x	not known		Myrberg et al. 1965
Sarotherodon galilaeus	x		x	x	Brown & Marshall 1978
Tilapia mariae		x	x		Albrecht 1966
Oreochromis mossambicus	x	x	x		Rodman 1966, Marshall 1971,1972, Lanzing 1974
Oreochromis niloticus	x		x		Bauer 1963
Simochromis babaulti	x	x	x	x	Nelissen 1978
Simochromis diagramma	x	x	x	x	Nelissen 1975,1978
Tropheus brichardi	x	x	x	x	Nelissen 1978
Tropheus duboisi	x	x	x	x	Nelissen 1978
Tropheus moorii	x	x	x	x	Nelissen 1977,1978

flections and reverberations (Myrberg & Spires 1972). Ambient aquarium noises also cause interference that can obscure the fine structure of a fish sound analyzed sonographically (Nelissen 1978, Rowland 1978). Another difficulty of aquarium studies is that it is possible that a fish's hearing could be damaged or altered due to background noises in aquaria generated by pumps, filters and other vibrations (e.g., Banner & Hyatt 1973, Popper & Clark 1976, Ha 1985, Cox et al. 1987, Myrberg 1990a,b). The effect of raising cichlids and other fishes in captivity (usually with young separated from parents and in heavily aerated aquaria) on their development of hearing, sound production and behavior is unknown.

The sounds produced by African cichlid species range in mean number of pulses per call from 9 to 43 and with mean call durations ranging from 181 to 1110 ms (Table 4). Cichlid courtship calls are similar to the pulsed calls produced by other fishes, especially reef pomacentrids (e.g. Myrberg et al. 1978, Lobel & Mann 1995). Playback experiments on pomacentrids have shown that these fish can behaviorally discriminate between conspecific and interspecific calls (Myrberg et al. 1978, 1986, Myrberg & Spires 1972, 1980, Spanier 1979). Gerald (1971) demonstrated that pulse rate within a call distinguish *Lepomis* (Centrarchidae) species. Winn (1964) developed a conceptual model of the structure of fish sounds showing that pulse repetition rate, pulse durations and sequence patterns are simple ways by which different species' calls could be identified

and used for species recognition (see also Fine et al. 1977, Myrberg et al. 1978).

Fryer & Iles (1972) predicted that sounds might play an important role in cichlid reproduction behavior. The simplest information that may be communicated by mere sound occurrence is mate location and readiness to spawn. The next level of complexity in communication maybe acoustic recognition of male size. Male size is correlated to the dominant frequency of his sound and females may be able to use this cue for mate assessment (Myrberg et al. 1993, Lobel & Mann 1995). The spectral basis for species recognition is unknown but probably involves a combination of acoustic and behavioral features possibly including pulse repetition rate, pulse amplitude variation, call repetition rate, number of pulses in a call, call duration, plus color pattern changes and swimming behavior. Conclusive demonstration of acoustic communication will require experimental playback of male sounds and quantitative measurement of female responses. The relative role of acoustics to other factors such as nest size, male size and behavior in the mate selection process remains to be determined.

Acknowledgements

Table 4. Variation in courtship and aggressive sounds by African cichlids.

African lake	Cichlid	Number of calls recorded	Mean (range) number pulses	Call duration, msec	Dominant frequencies, Hz	Reference
Chad & Tomba rivers	*Hemichromis bimaculatus*	23	42.6	Usually less than 500	ca 500	Rowland 1978
Tanganyika	*Haplochromis burtoni*	40	13 (5–37)	370 (230–1410)	320 (120–630)	Nelissen 1977
Tanganyika	*Simochromis babaulti*	28	26 (8–40)	590 (240–1470)	193 (125–500)	Nelissen 1978
Tanganyika	*Simochromis diagramma*	11	26 (16–37)	1110 (600–1700)	200 (100–200)	Nelissen 1978
Tanganyika	*Tropheus brichardi*	7	32 (9–92)	830 (250–2350)	ca 620	Nelissen 1978
Tanganyika	*Tropheus duboisi*	36	19 (3–33)	460 (70–1470)	407 (125–1250)	Nelissen 1978
Tanganyika	*Tropheus moorii*	46	20 (5–35)	400 (150–900)	840 (50–1250)	Nelissen 1977
Malawi	*Copadichromis conophorus*	127	10 (5–30)	181 (78–654)	471 (372–594)	this study
Malawi	*Tramitichromis* cf. *intermedius*	20	9 (6–12)	199 (120–304)	388 (305–480)	this study

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