

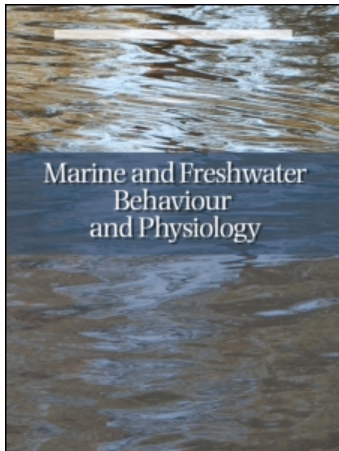
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SHORT COMMUNICATION

The association of visual and acoustic courtship behaviors in African cichlid fishes

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The cichlid fishes of Lake Malawi represent a prime example of a rapid evolutionary radiation via sexual selection. We show that in this group, acoustic communication significantly coincides with visual courtship displays. Specifically, individuals tend to use both multimodal and unimodal displays in successive courtship bouts. Behavioral analyses on six species of Malawian cichlids from two divergent genera revealed that five of the species use displays containing both an auditory and a visual component. *Metriaclima zebra* “*katale*” was the notable exception, along with a single individual of *Metriaclima lombardoi*, which utilized unimodal and multimodal displays with equal frequency. Taken together, these results highlight the importance of behavioral lability in multiple sensory signals at both the intra- and interspecific levels.

Keywords: acoustic; multimodal; communication; courtship; cichlid; *Metriaclima* spp.; *Melanochromis* spp.

Sexual selection relies on the exchange of sensory information when courting individuals assess and choose potential mates. Strong selection can lead to the exaggeration of traits resulting in extravagant phenotypes that are conspicuous to other individuals (as well as to the human observer). In systems with accentuated visual characteristics, observers often utilize these traits to identify individuals or to estimate fitness. The presence of a conspicuous signal in a given modality, however, rarely indicates that information from other sensory modalities is absent or unnecessary. Communication systems frequently rely on multiple signal types and modalities for effective displays (Rovner and Barth 1981; Narins et al. 2003).

The cichlid fishes of the African great lakes are a classic model of rapid species divergence through explosive radiation. The prevailing model to explain this species-richness is evolution via sexual selection that acts predominantly on male nuptial coloration. Visual sexual selection appears to be commonplace in many rift lake cichlids, from Lakes Malawi (Arnegard et al. 1999; Kornfield and Smith 2000; Allender et al. 2003), Victoria (Seehausen et al. 1997; Maan et al. 2004), and Tanganyika (Salzburger et al. 2006). However, there is little confirmation that the system is indeed exclusively visual. A variety of cichlids are known to produce

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acoustic signals, including those from Central and South America (Myrberg et al. 1965; Schwarz 1974, 1980), African riverine species (Myrberg et al. 1965; Amorim et al. 2003), and rift lake cichlids (Lobel 1998, 2001; Amorim et al. 2004). Moreover, Malawian cichlids emit calls with species-specific acoustic characteristics during courtship (Amorim et al. 2004, 2008; Ripley and Lobel 2004), similar to the marine damselfishes (Myrberg et al. 1978).

Along with acoustic qualities of the courtship call, Amorim et al. (2004, 2008) described a general correlation between calls and the “quiver” or “lead” portions of the male’s visual display. However, it is important to note that while a call is almost invariably accompanied by a quiver or lead, the converse is not necessarily true. Here we describe the preferential use of acoustic signals during courtship displays, and the extent to which this phenomenon can vary among individuals and species. In doing so, we demonstrate that the use of multimodal audiovisual courtship displays is variable between individuals, and not necessarily consistent even within species.

Six species were selected from two genera: *Metriaclima* (*Maylandia*) *zebra*, *Metriaclima callainos*, *Metriaclima lombardoi*, *Melanochromis auratus*, *Melanochromis johanni* (Eccles), and *Melanochromis cyaneorhabdos* (Bowers and Stauffer). Five males were used from each species except for *M. johanni* ($n=4$), *M. lombardoi* ($n=4$), and *M. callainos* ($n=2$). We utilized a number of stimulus females depending on availability (*M. auratus*, $n=4$; *M. johanni*, $n=3$; *M. cyaneorhabdos*, $n=3$; *M. lombardoi*, $n=3$; *M. zebra*, $n=2$; *M. callainos*, $n=2$). All individuals were wild-caught and acquired from a single locale whenever possible (assurance provided by Malawi Aquatics, Chipoka, Malawi), with the exception of three male *M. auratus*, which were captive-bred F₁ fish substituted because of mortality.

All animals were housed in isolated cages at the animal facility of Bowling Green State University (Ohio, USA). These cages were made of a submerged 29 cm × 19 cm × 18 cm plastic housing (Exo Terra Inc., Rolf C. Hagen Group, Montreal, Quebec, Canada) with a vented black lid and a series of ¼” holes along the upper rim for better water flow. Three sides of each shelter were covered with black plastic, and an 11 cm section of 5 cm diameter PVC pipe was added to provide structure. This housing offered both visual and physical isolation, which prevented social interactions between fishes (i.e. sound production by fishes was unlikely). The enclosures were distributed evenly in the reservoirs of two independent water trays (2.15 m × 0.79 m × 0.75 m reservoir and a 2.15 m × 0.79 m × 0.12 m flow table). Water temperature was maintained at 25C, with a 12-hour light cycle (from 8:00 to 20:00).

The trial arena consisted of a 0.90 m × 0.60 m × 0.60 m fiberglass tank with a front viewing pane (Aquatic Eco-Systems Inc., Apopka, FL, USA) mounted on a counterbalanced high-capacity vibration table (model # 68-561, Technical Manufacturing Corporation, Peabody, MA, USA). Runners were installed in the center of the tank for a pair of acrylic barriers; one was transparent with 6.35 mm diameter holes drilled in a grid to allow water flow and the other was a solid sheet of black acrylic. The bottom of the tank was covered with pea gravel and two small ceramic pots were placed mouth-to-mouth on each side of the runners to create caves for the fishes. A Bruel and Kjaer (Norcross, GA, USA) hydrophone (model #8103; sensitivity -211.6 dB re 1 V/μPa) was suspended above each cave, with each hydrophone running to an independent conditioning amplifier (Bruel and Kjaer Nexus

Conditioning Amplifier #2692-OS1; Bruel and Kjaer Charge Amplifier Type 2635). Output from amplified in-tank sounds was recorded directly to a memory card on a digital-to-audio recorder (Marantz Solid State Recorder PMD671, Mahwah, NJ, USA). Visual displays were filmed with a Sony Mini-DV camcorder (Model DCR-PC1000, Sony Corporation of America, New York City, NY, USA).

All trials comprised staged encounters between naïve pairs of mature conspecific males and females who had been socially isolated to ensure dominant status of the males. Before trial onset, animals were added to opposite sides of the arena with both transparent and opaque partitions in place. After a 2-h acclimation period, the opaque barrier was removed, leaving the transparent barrier in place to prevent physical damage to the fishes. The animals were allowed to interact for one hour while their behavior was recorded and acoustic data was gathered by the hydrophones on either side of the barrier. Since females were never found to produce sound, the hydrophone audio from the male's side of the tank was then dubbed over the video using iMovie HD (Apple Computer Inc., Cupertino, CA, USA). Times of behavioral onset and cessation were recorded using the program QT Movie Note Taker 0.5 (dvcreators.net, Los Angeles, CA, USA). The male quiver display, which is both easily identified and qualitatively conserved across the included species, represented the behavioral standard for visual courtship.

All courtship behaviors for an individual were recorded over the course of the trial then scored as a visual display without a call (assigned a value of 0) or a visual display accompanied by a call (assigned a value of 1). Calls were found to occur outside of visual displays, but at such a low frequency that they were dropped for all subsequent analyses (~9% of total behaviors). Two-tailed χ^2 analyses for each individual tested for a lack of preference for visual only, or a combined audiovisual courtship display. Pearson's χ^2 -value was used as a conservative measurement of behavioral bias.

Males of all species produced calls with physical characteristics consistent with previous reports for cichlids (reviewed by Lobel 2001), i.e. broadband signals (20–1200 Hz) with peak energy between 180 and 500 Hz. Short interpulse durations created uniform grunts, except for *M. zebra* and *M. callainos* where a rapid series of pulses resulted in clearly audible individual clicks.

Courtship of male *M. auratus* and *M. johanni* was exceedingly rare as their displays towards their female conspecifics were mostly aggressive in nature. Of the remainder, the majority of individuals preferred multimodal courtship displays, with *M. cyaneorhabdos*, *M. johanni*, *M. lombardoi*, and *M. callainos* all favoring vocal displays ($p < 0.05$; Table 1). In contrast, no calls were recorded in conjunction with a visual display in *M. zebra* ($n=40$). A single *M. cyaneorhabdos* and an individual *M. lombardoi* were also found to be primarily nonvocal ($p < 0.05$; Table 1). A single *M. lombardoi* displayed no preference for vocal or non-vocal displays (Pearson's $\chi^2 = 1.00$, $p = 0.32$; Table 1). The occurrence of behaviors for all individuals and their associated p -values are summarized in Table 2.

While it has been reported that acoustic signals in principle may accompany specific phases of the visual courtship (Amorim et al. 2004, 2008), this is the first study to statistically characterize the relationship between visual and acoustic behaviors and to describe variability in the patterns of intra- and interspecific usage. Individuals generally used multimodal displays comprising both acoustic and visual signal components. However, strictly visual displays are not uncommon, and are even favored by certain individuals (Table 1). The only species-specific pattern

Table 1. Summary of individual signaling preferences within each species as determined by Pearson's χ^2 . The "vocal" column indicates individuals that preferentially used multimodal courtship displays, while "nonvocal" denotes individuals who preferentially used only visual displays. Fish in the "indeterminate" column did not perform sufficient behaviors for statistical analysis.

Species	Vocal	Nonvocal	No preference	Indeterminate	No courtship	Total
<i>M. auratus</i>	0	0	0	1	4	5
<i>M. cyaneorhabdos</i>	2	1	0	2	0	5
<i>M. johanni</i>	1	0	0	3	0	4
<i>M. callainos</i>	1	0	0	0	1	2
<i>M. lombardoi</i>	2	1	1	0	0	4
<i>M. zebra</i>	0	3	0	1	1	5

Table 2. Frequency of behaviors for all individuals that courted during trials, as well as the p -value for Pearson's χ^2 .

Species	Individual	Courtship type		p -value
		Nonvocal	Vocal	
<i>M. callainos</i>	1	8	24	0.005
<i>M. lombardoi</i>	1	10	6	0.317
	2	14	5	0.039
	3	5	31	<0.001
	4	1	11	0.004
<i>M. zebra</i>	1	9	0	0.002
	2	6	0	N/A
	3	9	0	0.002
	4	16	0	<0.001
<i>M. auratus</i>	1	6	1	N/A
<i>M. cyaneorhabdos</i>	1	0	12	<0.001
	2	3	36	<0.001
	3	1	3	N/A
	4	20	1	<0.001
	5	2	0	N/A
<i>M. johanni</i>	1	7	26	<0.001
	2	0	5	N/A
	3	3	0	N/A
	4	0	4	N/A

emerged in *M. zebra* where none of the males combined acoustic and visual behaviors. One individual produced six calls without a corresponding visual display while clearing gravel from his territory, but never during the courtship phase. These particular fishes were *M. zebra* "katala," and this lack of multimodal behaviors may be a population-level effect, as this finding conflicts with prior reports by Amorim et al. (2004). Only a single individual from the species *M. lombardoi* employed the uni- and multimodal behaviors interchangeably. This fish raises the interesting possibility that the combination of multiple modalities in a single display is behaviorally labile. The male cichlid courtship repertoire appears to be neither

strictly unimodal nor multimodal (except for *M. zebra* “*katale*”). Rather, it commonly utilizes both systems over a series of courtship bouts. This idea of a behaviorally labile communication system raises questions relevant to the study of sexual selection, such as the possibility of hybridization (potentially a substantial problem in Malawian cichlids; Smith et al. 2003; Streebman et al. 2004) through overlapping signal arrays, or even dishonest communication (*sensu* Dawkins and Krebs 1978; Dawkins and Guilford 1991). We anticipate that further experiments explicitly designed to test these notions will prove rewarding.

One of the primary problems we encountered over the course of the experiment was a seeming lack of motivation for courtship behavior among the paired individuals, particularly in our two very aggressive species (*M. auratus* and *M. johanni*). This likely stemmed from the isolation-housing regime, which was effective in producing mature males with the normal color and behavioral phenotypes associated with territoriality and dominance. However, the females also developed hyper-aggressive territorial behaviors. Staged dyads including these females generally resulted in agonistic interactions at the expense, or complete disruption, of courtship. This greatly decreased our ability to collect data for the *Melanochromis*, and the possibility of multimodal communication in this genus remains.

In sum, this work firmly establishes both the importance and limits of acoustic signaling during cichlid courtship. Acoustic behaviors appear to augment visual displays, but are neither necessary nor sufficient for the courtship process. No individual was observed with courtship calls only, and many interactions occurred without them. As a common supplement to the conspicuous visual displays of courtship, acoustic signals are potentially subject to sexual selection, and the inter-individual variation observed lends credence to this contention. It is now clear, however, that the acoustic environment in which cichlid mate-choice experiments are performed is an important variable to be considered.

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