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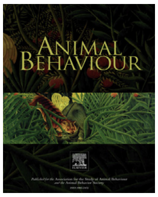

Underwater noise impairs social communication during aggressive and reproductive encounters

Julie M. Butler*, Karen P. Maruska

Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, U.S.A.

A R T I C L E I N F O

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Human-generated noise pollution is of global concern, as designated by the World Health Organization (WHO, 2011, *Burden of disease from environmental noise: Quantification of healthy life years lost in Europe*. https://www.who.int/quantifying_ehimpacts/publications/e94888/en/). Increases in shipping, sonar use, pile driving, and more have all contributed to a rise in ambient underwater sound levels. Unfortunately, continuous low-intensity sounds, like shipping noise, are pervasive in shallow-shore environments where many social species live and correspond to the frequency ranges at which many fishes produce and detect acoustic stimuli. Noise has the potential to alter the sender's production of the signal, mask the signal itself (if acoustic), or change the receiver's physiology. We hypothesized that continuous tonal noise would impair social interactions and communication. To test this, we used highly social African cichlid fish, *Astatotilapia burtoni*, to examine inter- and intrasexual interactions that occurred in a control or noisy environment (pure tones of 100–2000 Hz). During reproductive interactions, we found that males changed the location of their courtship behaviours. Instead of producing courtship quivers (and associated sounds) immediately next to gravid females, males produced these behaviours inside their spawning shelter. This change in location decreases the likelihood of the female detecting it. Also detrimental to acoustic communication, we found that noise-exposed gravid females had lower hearing sensitivity at 100–200 Hz, a major component of male courtship sounds. In addition, males changed their visual displays during male–male territorial interactions such that they spent more time with their eyebar displayed, suggesting an increase in visual signalling. Together, these data indicate that noise may impact all three components of social communication: signal production, signal reception and the signal itself, and highlights a possible cross-modal impact of noise on visual signalling. Subtle changes to social behaviours and communication, rather than dramatic effects such as injury or mortality, are important to evaluating sublethal impacts of noise on reproductive success and species survival.

Communication is a vital aspect of all social interactions. Animals rely on signals encoding information about the sender's species, sex, motivation, reproductive state and identity. Communication involves a sender producing a stimulus that encodes information and a receiver using this information to make a decision on how to appropriately respond (Bradbury & Vehrencamp, 1998). For communication to be effective, the signal itself, the receiver's sensory physiology and the receiver's response must be in tune with the environmental conditionals that carry the signal (Cole, 2013). Disruption of this communication can have detrimental impacts on both the sender and receiver. Unfortunately, anthropogenic (human-made) noise is now a pervasive pollutant to almost all aquatic and terrestrial environments (Halfwerk & Slabbekoorn, 2015). Shipping travel, sonar use and oil exploration all contribute to the rise in ambient underwater sound levels in the frequency range that most fishes produce and detect acoustic stimuli (Scholik & Yan, 2001, 2002a, 2002b; Board, 2005; Crovo, Mendonça, Holt, & Johnston, 2015; Purser & Radford, 2011; Radford, Kerridge, & Simpson, 2014; Vasconcelos, Amorim, & Ladich, 2007). Anthropogenic noise is linked to changes in hearing capabilities (Casper et al., 2013), schooling and shoaling behaviours (Herbert-Read, Kremer, Bruintjes, Radford, & Ioannou, 2017), development (Davidson, Bebak, & Mazik, 2009; Nedelec, Simpson, Morley, Nedelec, & Radford, 2015), learning and memory (Ferrari et al., 2018), stress physiology (Anderson, Berzins, Fogarty, Hamlin, & Guillette, 2011; Crovo et al., 2015), foraging (Bracciali, Campobello, Giacoma, & Sara, 2012; McLaughlin & Kunc, 2015), predator avoidance (Chan, Giraldo-Perez, Smith, &

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* Correspondence and present address: J. M. Butler, Biology Department, Stanford University, 371 Jane Stanford Way, Stanford, CA 94305-5020, U.S.A.
E-mail address: jmbutler@stanford.edu (J. M. Butler).

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Blumstein, 2010) and social behaviours (Algera, Gutowsky, Zolderdo, & Cooke, 2017; Bruintjes & Radford, 2013, 2014; de Jong, Amorim, Fonseca, Fox, & Heubel, 2018a; Sebastianutto, Picciulin, Costantini, & Ferrero, 2011) in diverse fish species. However, there remains a paucity of research on how anthropogenic noise impacts social communication.

Over 800 species of phylogenetically diverse fishes are known to produce sounds, mainly during reproduction (Fine & Parmentier, 2015). Acoustic signals are typically produced by males during courtship and can provide females with information on male size and condition for use during mate choice. Most courtship sounds have dominant energy at low frequencies and are intended for relatively close-range communication (Amorim, 2006), making them susceptible to acoustic masking from increased background noise. For example, darters, gobies and sculpins typically produce pulsed sounds under 200 Hz that are almost always associated with agonistic or reproductive interactions and only function over a distance of a few centimetres (Lugli, Yan, & Fine, 2003; Zeyl et al., 2016). Toadfish and midshipman males establish nests in shallow intertidal zones and form choruses to attract gravid females. Although their sounds are relatively loud (125 SPL dB re: 1 μPa; Barimo & Fine, 1998), the attenuation in shallow water means females only respond to sounds produced within 13 m (Alves, Amorim, & Fonseca, 2016; Fine & Lenhardt, 1983). The ability to recruit reproductively receptive females to a spawning territory is extremely important for site-attached animals living in noisy acoustic environments.

Any movement underwater will inevitably generate hydrodynamic stimuli that can be detected by the lateral line system of nearby fish. Fish perform many social behaviours that involve fin and body motions (Butler & Maruska, 2016), termed ‘signal movements’ by early neuroethologists. For example, an aggressive lateral display involves one fish orienting parallel or perpendicular to an opponent, fully erecting its dorsal, anal and caudal fins, and distending its jaw to create a visual display of larger size. During this visual display, many fishes also shake their body, gently or vigorously. This behaviour, and many other common aggressive and reproductive behaviours, generate water movements that can be detected by conspecifics. Body and tail movements generate hydrodynamic flow fields consisting of low-frequency stimuli (<10 Hz) coupled with higher-frequency acceleration components (Bleckmann, Breithaupt, Blickhan, & Tautz, 1991), indicating that these stimuli can stimulate both superficial and canal neuromasts of the lateral line system. Any disruption of mechanosensory communication could have detrimental effects on fish social communication and ultimately reproductive success and species persistence (Butler & Maruska, 2016).

Playback of boat noise or white noise affects hearing capabilities and can result in a physiological stress response (Casper et al., 2013; Crovo et al., 2015). Anthropogenic noise also affects territorial behaviours in gobies (Sebastianutto et al., 2011), nest maintenance and defence behaviours in cichlids (Bruintjes & Radford, 2013), and social communication and spawning success (de Jong et al., 2018a). While studies have examined the impact of noise on behaviour and on signal production or sensory capabilities individually, no study has tested for noise-induced impacts on social behaviours and communication as a whole. By examining noise-induced impacts on multiple components of social communication, we identify subtle changes that can have major consequences for predator avoidance and reproductive success. We used a tonal noise, as opposed to a broadband or naturalistic sound, to test for frequency-dependent impacts of noise on social behaviours and communication. These types of subtle noise-induced changes to behaviour and communication can serve as early indicators of potentially harmful impacts of noise exposure on fishes. Subtle changes, as opposed to major organ damage or even death, are possibly more important for management and conservation efforts.

The African cichlid fish *Astatotilapia burtoni* is an excellent system to investigate the impacts of underwater noise on social interactions. Their social behaviours and communication are well documented and described (Fernald & Hirata, 1977; Maruska & Fernald, 2010, 2018). Male *A. burtoni* live in a territorial system as two main phenotypes on a continuum: dominant/territorial and subordinate/nonterritorial. They are able to rapidly and reversibly switch between phenotypes depending on their social environments (Maruska & Fernald, 2011, 2013). Dominant males actively defend their spawning territory from other males using a variety of agonistic behaviours, such as chases, bites, lateral displays and frontal threats (Fernald & Hirata, 1977). While there is no evidence for intentional sound production during agonistic interactions, these behaviours do produce hydrodynamic stimuli, and detection of these water movements are essential for mutual assessment and fight escalation (Butler & Maruska, 2015). During courtship, males use visual, acoustic (both auditory and hydrodynamic) and chemical signals to entice females to their territories for spawning (Maruska, Ung, & Fernald, 2012; Maruska & Fernald, 2012). Dominant males actively court females using body quivers, tail waggles and leads. During a body quiver, a male displays his anal fin to a gravid female while vigorously shaking his body. This is often followed by exaggerated waggles of the tail while leading the female back to the spawning territory. Like aggressive behaviours, male courtship behaviours produce water movements that females can potentially use for mate choice. Dominant *A. burtoni* males also produce facultative courtship sounds during reproductive body quivers (broadband, with 300–700 Hz peak frequency), and gravid females prefer males associated with courtship sounds (Maruska et al., 2012). Larger males produce more courtship quivers with sounds, and body size correlates with mean peak frequency of the sound, indicating that acoustic signals are an honest indicator of male quality. Because *A. burtoni* rely on acoustic communication during social interactions, it is possible that underwater noise could interfere with this communication and therefore alter social behaviours.

Here, we examined the impact of underwater tonal noise on territorial male–male interactions and reproductive male–female interactions, both of which are necessary for species persistence. In both contexts, fish were less likely to interact with each other in a noisy environment compared to controls. When they did interact, fish performed the same number of behaviours, but how they used them (i.e. sequence, timing) differed between the sound conditions. Finally, females had reduced hearing capabilities, were less responsive to male courtship attempts and had a lower incidence of spawning during noise exposure. Overall, these data indicate that tonal noise has negative impacts on social behaviours, with changes to signal production and ultimately decreased social communication. Disruption of social communication during these vital behaviours likely has negative impacts on predation rates, reproductive fitness and species persistence.

METHODS

Experimental Animals

Laboratory bred *A. burtoni* were maintained in community aquaria at conditions simulating their natural environments (pH = 7.6 – 8.0; 28–30 C; 12:12 h light:dark cycle). Adults were fed cichlid flakes daily and brine shrimp twice weekly. All community aquaria contained two to three partial terracotta pots to serve as spawning territories. A total of 56 individuals were used (mean ± SE: standard length = 44.75 ± 6.18 mm; body mass: 2.503 ± 0.826 g).

Sound Exposure Protocol

All behaviour experiments occurred in 38-litre glass aquaria placed on several layers of foam insulation to isolate them from outside vibrations. Each tank (49.5 25.4 29.2 cm) was divided into two compartments by an opaque acrylic divider (front compartment: 35 cm; back compartment: 14.5 cm). The back compartment contained an underwater speaker (UW-30, frequency response 100 Hz to 10 kHz). The submerged speaker was placed in a separate compartment from the behaviour trials because males used the inside of the speaker or the area immediately behind the speaker as their territory when sound was not being broadcast. The speaker was suspended from a PVC frame above the tank so that no part of the speaker touched the tank. All behaviour experiments occurred in the front compartment.

To create a 'noisy' environment, we created a sound file in Audacity v.2.1.1 (http://audacityteam.org/) composed of random pure tones ranging from 100 Hz to 2000 Hz (the hearing range of *A. burtoni*; Maruska et al., 2012). Tone order and duration (0.5–4.0 s) were randomized. Each sound file was approximately 5 min but looped for the duration of the 30 min behaviour trial. Sound files were amplified (TOA, CA-160) before being played through the underwater speaker. The amplifier was adjusted so that the sound level was ~140 SPL (sound pressure level) dB re: 1 μPa immediately above the territory. During control trials, all equipment was present, but no sound file was played through the speaker.

To characterize the two sound conditions, a calibrated hydrophone (HTI-94, High Tech, Inc., Gulfport, MS, U.S.A.; sensitivity -163.7dB re: 1 V/μPa; frequency response 2 Hz to 30 kHz) was suspended in the water immediately above the spawning shelter. We recorded during the playback of tonal noise and ambient control conditions. We also measured spectral densities of the sound file itself that was used for the playbacks to visualize how the intended sound file that was sent to the speaker differed from how it was received by the hydrophone within the small tank. Spectral level densities were created in Audacity (FFT analysis, Hann window, 1024 points; Fig. 1). In addition, we generated spectrograms of the two sound conditions and the original sound file. Spectrograms reveal that the sound file was much more broadband than intended.

We chose to use pure tones within the hearing range of *A. burtoni* (Maruska et al., 2012) instead of boat playback or broadband noise because we hypothesized that tonal noise would be easier to characterize and reproduce within aquaria. Sound playback in small aquaria cannot adequately mimic natural sound conditions, even under ideal conditions (Akamatsu, Okumura, Novarini, & Yan, 2002). The use of 100–2000 Hz tones is within the output range of the speaker and limits resonant frequencies associated with playback in a small aquarium. In addition, this allowed us to examine whether or not there was a frequency-dependent impact on behaviours. While the sound stimulus used in this study does not represent a natural stimulus (i.e. playback of motorized boat), it has similar characteristics including predominantly low frequencies. Unfortunately, when played in the experimental set-up, the tonal noise file produced a predominately broadband sound, further highlighting the difficulties in sound playback in small aquaria. Importantly, anthropogenic noise associated with boating has been recorded in Lake Tanganyika (Bruintjes & Radford, 2013, 2014), the natural habitat for this species, providing natural and ethological rationale for this study.

Aggressive Behaviour Protocol

To examine the impact of underwater tonal noise on territorial interactions, we induced aggressive interactions between two males occurring in either silent ($N = 7$ trials) or noisy ($N = 9$ trials) conditions. To create an equal-opportunity territorial dispute (as done in Butler & Maruska, 2015), we divided the front compartment of the experimental tank into two parts using an opaque blue barrier placed perpendicular to the speaker barrier (Fig. 2a). A quartered terracotta pot was placed on either side of the barrier so that a single territory was split by the barrier. Dominant males were identified from community tanks based on coloration (e.g. eyebar, bright yellow coloration) and display of stereotypical aggressive behaviours for >1 week. One male was placed on each side of the experimental tank and allowed to acclimate for 2 days. Males were always size-matched (within 10% of standard length) and fin-clipped (middle or back of dorsal fin) for identification. On the morning of the trials, a video camera was set up in front of the tank. The sound file or control silence was started, and recorded for 5 min. The barrier was then removed and the pots were repositioned to form a single territory that the two males fought over. Each trial lasted 30 min from when the barrier was removed.

We used the above experimental paradigm (5 min of acclimation, followed by 30 min of behaviour trials) after performing several pilot experiments testing different exposure protocols. We performed some experiments where fish were pre-exposed to tonal noise 24 h before the trial or acclimated to noise for ~1 h before the experiment ($N = 3$ trials each). In both cases, behaviour trials appeared similar to those where fish were only acclimated to tonal noise for ~5 min. We also pre-exposed animals to noise but turned the noise off immediately before the start of a trial ($N = 3$ trials). This appeared to have little effect on the fish. While it is possible that fish simply had a stress response to the novel stimulus, it is impossible to decouple inherent physiological processes (i.e. stress response) from changes in the soundscape alone. To minimize the abrupt nature of turning on the tonal sound file, the volume on the amplifier was initially turned off and slowly raised to the desired level.

Videos were later scored by an observer blind to sound condition. We quantified stereotypical male aggressive behaviours, including lateral displays, frontal threats, bites, lunges, rams and mouth fighting (Table 1). Behaviours were classified as either noncontact (e.g. lunge, frontal threat, lateral display) or contact (e.g. bite, ram) since use of noncontact behaviours is mediated by mechanosensory signalling (Butler & Maruska, 2015). Latency to begin fighting was defined as the time between when the pots were repositioned and when reciprocal aggressive behaviours were performed. Fight conclusion was determined based on criteria similar to that previously used (Butler & Maruska, 2015). The winner had to perform at least three dominance behaviours and either enter the pot at least three times in a 1 min period or stay in the pot for >10 s. The loser had to fade his eyebar and other typical male coloration and perform submissive behaviours (e.g. flee, position of inferiority). Males will typically fight shortly after the barrier removal and have a single fight, after which one male emerges as the winner and spends the duration of the trials chasing and being aggressive towards the losing fish (Butler & Maruska, 2015). However, here, we observed that fights occurring during noise trials often occurred in bouts without the fight conclusion criteria being met. As such, we calculated fight duration based on the above criteria as well as the actual time spent fighting. A fight bout was considered over if neither fish performed a single aggressive behaviour for >30 s. Interbout interval was calculated as the time from the last aggressive behaviour to the next reciprocal exchange of behaviours. By subtracting the total interbout interval

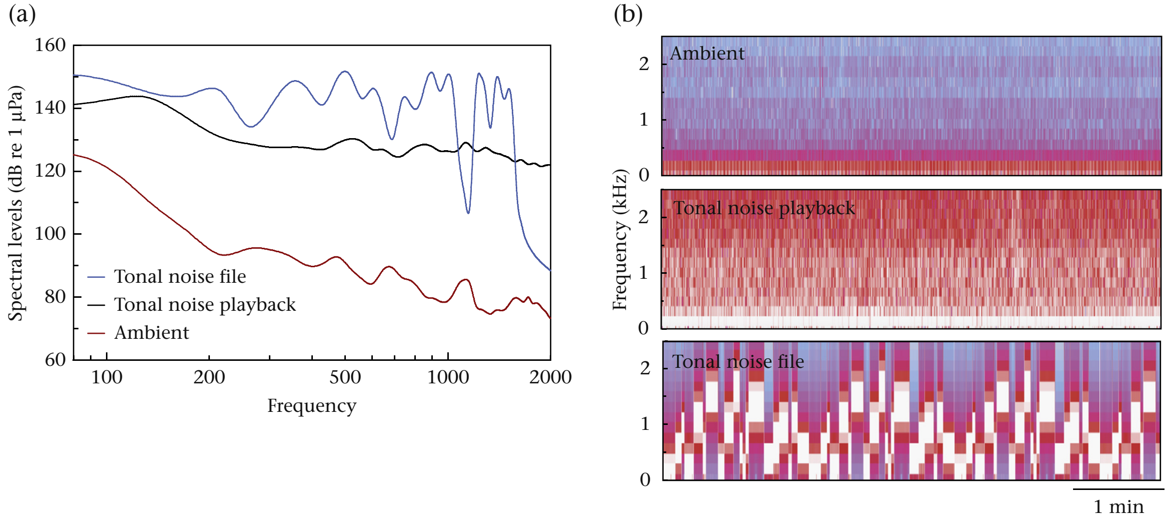

Figure 1. Spectral densities and spectrograms of tonal noise playback and ambient conditions. (a) A hydrophone was positioned immediately above the spawning shelter and used to record ambient control conditions and sound playback. Spectral level densities were created in Audacity (FFT analysis, Hann window, 1024 points) for the tonal noise file itself, recording of tonal noise playback and recording of ambient conditions. (b) A spectrogram was generated for the recorded sound conditions (ambient, top graph; noise, middle graph) and the sound file itself (bottom graph). White represents the highest power while blue represents the lowest power. Due to the acoustics of a small aquarium, the tonal noise file was more of a broadband sound.

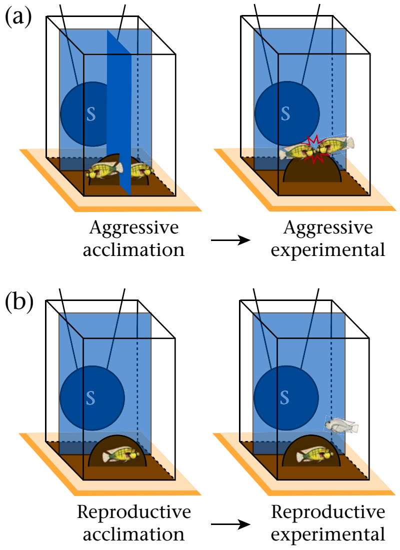

Figure 2. Experimental paradigm to induce aggressive (a) and reproductive (b) interactions. (a) During acclimation, the front experimental compartment was divided into two equal compartments, each housing a quartered terracotta pot and dominant male. After 2 days of acclimation, the barrier was removed and the pots were repositioned to form a single territory over which the males would fight. (b) The front experimental compartment housed a single halved terracotta pot to serve as a spawning territory for the dominant male. After 2 days of acclimation, a gravid female was added to the front compartment. In both set-ups, the back compartment housed the submerged underwater speaker (S) that was suspended from above the tank and hidden from view by a blue opaque barrier.

time from total fight duration, we calculated the actual time spent fighting.

In addition to typical aggressive behaviours, we quantified freezing/stress behaviours. This was defined as the fish remaining stationary in the water and flaring all of its fins. Fish also had a dark eyebar and vertical banding on the trunk during this behaviour. We also quantified the amount of time spent with the eyebar displayed. To measure mutual assessment, we quantified the time fish spent within one body length of each other without performing other behaviours (Butler & Maruska, 2015).

To test for frequency-dependent effects of noise on social and stress behaviours, we aligned the sound file to a raster plot of behaviours and quantified the number of behaviours in four different frequency ranges. We binned frequencies together as <200 Hz, 200–500 Hz, 500–1000 Hz and >1000 Hz. We quantified the number of stress and aggressive behaviours performed during each frequency category. For reproductive interactions (see below for details), we quantified the number of male courtship behaviours and displaced aggressive behaviours and female positive responses to male courtship behaviours that occurred in each frequency range. We also quantified which frequency range was being played when courtship or spawning bouts started. Importantly, we aligned behaviours to the sound file, not the recording of the sound playback. Because the intended sound file was more broadband than intended, it is possible that frequencies played and received by the fish differed from the intended frequency. Frequency bins were chosen because each category of frequencies was more easily distinguished from the other bins, even if they were not distinguishable within a frequency range.

Reproductive Behaviour Protocol

To examine the impact of tonal noise on reproduction, we induced reproductive interactions between a male and female during noise and control conditions ($N = 6$ trials per condition). The abovementioned experimental tank and sound file was used to create a noisy environment. Dominant males were selected from community tanks, placed in the front compartment of the experimental tank (Fig. 2b) and allowed to acclimate for 2 days. On the morning of the trials, an ovulated female was visually identified from community tanks based on a swollen abdomen, slightly distended jaw, protruding urogenital papilla and actively courting males. Once the female was identified, the noise playback was started and the female was quickly transferred to the front compartment of the experimental tank. A video camera was positioned in front of the tank and recorded for 30 min after the female was added to the tank.

Table 1
Aggressive and reproductive behaviour definitions

Behaviour	Definition	Sex	Context
Bite/ram	With mouth open (bite) or closed (ram), one fish quickly hits flank of other fish	M	A
Lunge	Rapid forward movement towards other fish	M	A
Lateral display	Fish flares all fins, distends jaw and gently vibrates body; often oriented perpendicular in front of other fish	M	A
Mouth fight	Two fish grasp jaws and gently push/pull	M	A
Frontal threat	While facing opponent, fish distends jaw and flares operculum	M	A
Chase/flee	One fish rapidly swims behind the other	M/F	A/R
Pot entry	Fish enters into halved terracotta pot	M/F	A/R
Dig	Fish picks up gravel from inside pot and spits outside of the shelter	M	A/R
Quiver	With anal fin displayed, fish rapidly vibrates body; dorsal fin often depressed against body	M	R
Tail waggle	Caudal fin exaggeratedly moved back and forth	M	R
Lead	Swimming in front of female and immediately swimming towards spawning territory; often accompanied with tail waggle	M	R
Spawning	Male prods female urogenital opening to stimulate egg release, female picks eggs up into buccal cavity, then nips at male anal fin	M/F	R
Circling	Male prodding and female nipping behaviours, but no egg release	M/F	R
Time spent within one body length (BL)	Both fish within one body length of each other but not performing any behaviours	M/F	A/R
Displaced aggressive behaviour	Bite, ram or lunge behaviour directed at an inanimate object	M/F	A/R
Stress flare	Fish stops swimming, flares all fins and displays vertical black banding; jaw does not distend and no body vibrations present	M/F	A/R

Some behaviours are typically only performed by males (M) while others are performed by both sexes (M/F). Behaviours are further classified as aggressive (A) or reproductive (R), but some behaviours are observed in both contexts.

We quantified stereotypical male courtship behaviours and female responses to each behaviour (Butler et al., 2019). For males, we quantified the number of body quivers, tail waggles and leads as overt courtship behaviours (see Table 1 for behaviour details). We also quantified the number of digs (territory maintenance) and the number of bites and chases that males directed at the females. We qualified female behaviour as ‘positive’, ‘negative’, or ‘no response’ to each male behaviour or string of behaviours (see below for behaviour descriptions). If the female oriented towards or followed the male behaviour within 1 s, it was classified as a positive response. Negative responses were defined as orienting away from the male or swimming away from him within 1 s of his behaviour. No responses were classified by the lack of a positive or negative response. For both fish, we quantified the amount of time spent within the spawning shelter (halved terra cotta pot) and against the front wall of the experimental tank, which was farthest from the speaker. The number of aggressive displays (e.g. bites, frontal threat) by the males to the back, speaker wall or other tank component (e.g. airstone, filter) was also quantified as displaced aggressive behaviours. Finally, we quantified the number of circling and spawning bouts of the pair, as well as the time spent circling and spawning. During spawning, females release eggs on the substrate, pick them up into their mouth, then nip at the male's anal fin to induce sperm release. Then the male gently prods/nips at the female to release more eggs, creating a ‘circling’ movement between the two fish where they alternate nipping at each other. Circling involves the same circular movements but does not involve egg release from the female.

Male *A. burtoni* are very behaviourally active during reproductive interactions and tend to perform multiple courtship behaviours within quick succession. For example, the most commonly seen male courtship behaviour sequence is a body quiver that transitions into a tail waggle, which occurs as the male leads the female back to the pot. As such, in addition to quantifying individual behaviours, we also classified them as single behaviours or strings of behaviour (2 behaviours, 3 behaviours, or 4+ behaviours). To do this, we calculated the interbehaviour interval and used a cutoff of 1 s. Any behaviour occurring within 1 s of the previous behaviour was classified as a string. Only overt courtship behaviours (i.e. quivers, waggles, leads, pot entries) were included in the string analysis.

Auditory-evoked Potentials

To determine how exposure to anthropogenic noise impacts hearing capabilities, we measured hearing thresholds using auditory-evoked potentials (AEP) as done previously (Maruska et al., 2012). Briefly, fish were anaesthetized in 0.1% benzocaine in fish water, immobilized with an intramuscular injection of pancuronium bromide (~0.001 mg per gram of body mass) and restrained in a mesh harness suspended from a PVC frame above the experimental tank on a vibration isolation platform (Fig. 3). Fish were suspended in the centre of the circular experimental tank (36 cm high, 30 cm diameter) and positioned just below the water surface and ~15 cm above the underwater speaker (UW-30) that was partially buried in gravel at the bottom of the tank. A gravity-fed water system connected to a small tube in the mouth was used to ventilate fish during the experiments. Electrodes (stainless-steel subdermal electrodes, Rochester Electro-Medical, Inc., Tampa, FL, U.S.A.) were sealed on the ends with nail polish so that ~1 mm of metal was exposed at the tip. A recording electrode was positioned in the dorsal musculature directly above the braincase, a reference electrode was placed beneath the skin between the eyes and a ground wire was placed in the tank water.

Sound stimuli were generated by a CED Micro3 analogue to digital converter and attenuator, controlled with Spike2 v.8.06 software (Cambridge Electronic Design Ltd, Cambridge, U.K.), amplified and played through the underwater speaker. We tested eight frequencies that encompass the hearing range of *A. burtoni* (Maruska et al., 2012): 100, 200, 300, 400, 500, 600, 800 and 1000 Hz. Each stimulus consisted of 2000 repetitions of 20 ms pulses (alternating phase) with an interpulse interval of 100 ms. For each frequency, stimuli were played at suprathreshold levels and decreased incrementally by 5 dB until an AEP response was no longer observed. Sound levels were calibrated by placing a hydrophone in the experimental tank at the position normally occupied by the fish head, presenting the sound stimuli (without phase alternation), and measuring the RMS voltage at each test frequency and intensity. AEPs were differentially recorded, amplified (10 000), filtered (0.1–10 000 Hz) and then digitized by the CED A-D system. Threshold at each frequency was defined as the lowest sound level at which a repeatable AEP response was observed and power spectrum analyses (FFT, Hanning Window, 512 or 1024 points) showed peaks 3 dB above background levels (Kibele, Montgomery, & Radford, 2019; Mélotte, Parmentier, Michel, Herrel, & Boyle, 2018) at twice the stimulus frequency (due to oppositely oriented hair cells).

Because gravid females have the best hearing sensitivity and are the primary intended receivers of acoustic communication, we only assessed the impact of noise on hearing capabilities in gravid females. Females were placed in the experimental tank and played the previously described tonal noise file (as described above; Fig. 2) or control for 3 h. Immediately after the 3 h exposure, AEPs were performed.

Ethical Note

All experiments were performed in accordance with the recommendations and guidelines stated in the National Institutes of Health (NIH) Guide for the Care and Use of Laboratory Animals (National Research Council, 2011). All animal care and collection was approved by the Institutional Animal Care and Use Committee of the Louisiana State University, Baton Rouge, Louisiana, U.S.A. (IACUC protocol No. 14–082 and No. 18–001). Animals were checked daily for welfare. All animals were allowed to live in the laboratory after the behaviour experiments, and the experimental conditions (i.e. exposure to noise playback) only caused short-term behavioural impacts during the noise stimulus. No experimental conditions caused lasting impacts on animals. Fin clipping was done by immersing fish in ice-cold fish water for ~30 s and wrapping the fish in a wet cloth. The dorsal fin was then pulled erect and a small triangle (~5 mm width) was removed from either the middle or caudal portion of the edge of the fin using sterile surgical scissors. Fish were immediately placed back into the experimental set-up for recovery and acclimation. Fin clipping did not cause any distress for the animals and is commonly used as a mode for distinguishing individuals.

Statistics

All statistics were performed in SigmaPlot 12.3 (SPSS Inc., Chicago, IL, U.S.A.) or IBM SPSS 25 (IBM, Armonk, NY, U.S.A.). We used Student's *t* tests (two tailed) to compare data between the two sound conditions within each behavioural condition. No outliers were detected via Grubbs outlier test. If data did not pass normality or equal variance testing, it was log-, ln- or square-root transformed. If data still did not pass normality and/or equal variance, nonparametric testing was used. For comparison of aggressive and stress-related behaviours in aggression trials, we used a linear mixed model (LMM) because the two fish in a trial were not independent of each other. Winner or loser was a repeated within-subject factor, and sound condition (control versus noise) was a between-subject fixed factor. Individual subjects and trial identity (ID) were included as random effects and Tukey's test was used to determine post hoc differences. To compare the behaviour strings used by the males during reproduction, we used a repeated measures ANOVA with the number of behaviours in the string as a repeated within-subject factor and sound condition as the between-subject factor. This was followed with Tukey's post hoc testing to isolate differences. We tested for frequency-dependent impacts on behaviour using a repeated measures ANOVA, with frequency bin as the repeated factor within each trial/individual. To test for noise-induced hearing loss, a two-way repeated measures ANOVA was used with frequency as the repeated within-subject factor and sound condition as the between-subject factor.

RESULTS

Noise Exposure Impacts Fight Timing but Not Overall Aggressiveness

All seven control trials of the male–male interaction context resulted in a territorial fight that occurred shortly after the barrier removal. However, only seven of the nine tonal noise trials resulted in a fight. Latency to initiate a territorial fight was longer in noise trials (mean ± SEM = 12.472 ± 3.59 min) compared to control trials (2.679 ± 1.153 min) (Student's *t* test: log-transformed: $t_{14} = -3.298$, $P = 0.005$; Fig. 4a). However, during the longer latency time, fish did not perform more mutual assessment behaviours ($t_{14} = -0.742$, $P = 0.470$; Fig. 4b). Neither time spent fighting ($t_{12} = 0.507$, $P = 0.621$; Fig. 4c) nor fight duration ($t_{12} = -1.705$, $P = 0.114$; Fig. 4d) differed between the sound conditions. Fish fought in bouts

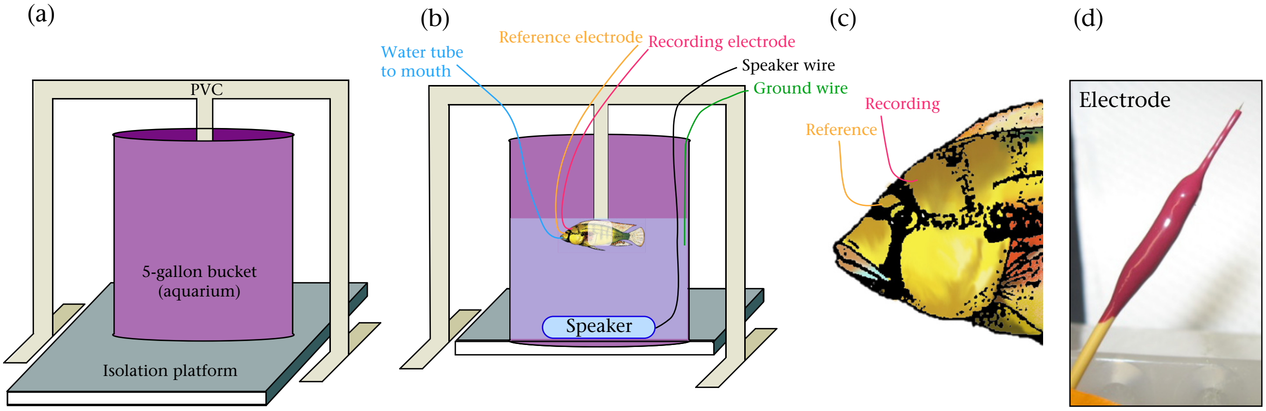

Figure 3. Experimental set-up used for auditory-evoked potentials. (a) The aquarium was placed on an isolation platform and a PVC frame was used to suspend the fish in water above an underwater speaker. (b–d) The fish was ventilated by a gravity-fed water system. Recording (red) and reference electrodes (orange) were placed above the brain case and beneath the skin between the eyes, respectively (c), and a ground wire (green) was placed in the tank water. (d) Electrodes were coated with nail polish with ~1 mm of metal exposed at the tip.

rather than in one succinct fight (t_{12} = -3.481, $P = 0.005$; Fig. 4e). All control trials took place in one single fighting bout. In contrast, noise trials involved 4.286 ± 0.944 fighting bouts. The average time between fighting bouts was 43.950 ± 5.921 s. The increased latency to fight and the change in fight structure increased fight resolution time during tonal noise (log-transformed: t_{12} = -3.829, $P = 0.002$; Fig. 4f).

Although fight structure differed between the sound conditions (Fig. 4g, h), there was no significant difference in the number of aggressive behaviours (LMM: outcome: $F_{1,14} = 37.934$, $P < 0.001$; sound: $F_{1,14} = 1.886$, $P = 0.834$; outcome sound: $F_{1,14} = 0.045$, $P = 0.834$; Fig. 5a) or the type of aggressive behaviours (LMM: outcome: $F_{1,14} = 2.631$, $P = 0.149$; sound: $F_{1,14} = 5.105$, $P = 0.056$; outcome sound: $F_{1,14} = 0.009$, $P = 0.925$; Fig. 5b) between the sound conditions. Winners had a higher aggressive score than losers ($P = 0.001$) in both sound conditions. Fish in the tonal noise condition performed more stress behaviours, like freezing and flaring all fins, than fish in control trials independent of fight outcome (LMM: outcome: $F_{1,14} = 0.523$, $P = 0.482$; sound: $F_{1,14} = 16.102$, $P = 0.001$; outcome sound: $F_{1,14} = 0.624$, $P = 0.443$; Fig. 5c). Noise-exposed fish also spent more time with their eyebar displayed than control individuals (LMM: outcome: $F_{1,14} = 28.691$, $P < 0.001$; sound: $F_{1,14} = 27.276$, $P < 0.001$; outcome sound: $F_{1,14} = 29{,}912$, $P < 0.001$; Fig. 5d). In control animals, eyebar time was dependent on winning or losing the fight, with winners displaying their eyebar more than losers, but outcome had no effect on eyebar time in noise trials.

Noise Affects Female and Male Reproductive Behaviours

Stereotypical male courtship behaviours were not impacted by tonal noise. Males performed similar numbers of body quivers (Student's t test: $t_{10} = 1.439$, $P = 0.181$), tail waggles ($t_{10} = 0.607$, $P = 0.558$), leads (Mann–Whitney U test: $U = 10$, $N_1 = N_2 = 6$, $P = 0.240$) and nips towards the female (Student's t test: t_{10} = -1.500, $P = 0.172$). Males also did not change their territory maintenance (digging out the territory: Mann–Whitney U test: $U = 9.50$, $N_1 = N_2 = 6$, $P = 0.180$). While the total number of courtship behaviours did not change (Student's t test: $t_{10} = 0.851$, $P = 0.415$; Fig. 6a), the location where the males performed these behaviours differed between the sound conditions. During noisy conditions, males performed more behaviours inside the pot (41.476 ± 10.449%) compared to control conditions (12.300 ± 3.331%; t_{10} = -3.708, $P = 0.004$; Fig. 6b), but they did not spend more overall time in the pot ($t_{10} = 0.959$, $P = 0.360$ Fig. 6c).

Under control conditions, males typically perform behaviour strings in quick succession (e.g. body quiver, tail waggle, lead). To examine whether this was impacted by tonal noise, we classified behaviours as occurring as a single event or in strings of two, three, or four or more behaviours. Although the total number of courting events (after accounting for behaviour strings) did not change ($t_{10} = 0.192$, $P = 0.852$; Fig. 6d), males altered how they performed the behaviours in relation to other behaviours. During noisy conditions, males perform more single behaviours (t_{10} = -5.647, $P < 0.001$) than males in control trials (Fig. 6e). However, males in control trials perform more strings of behaviours than males in

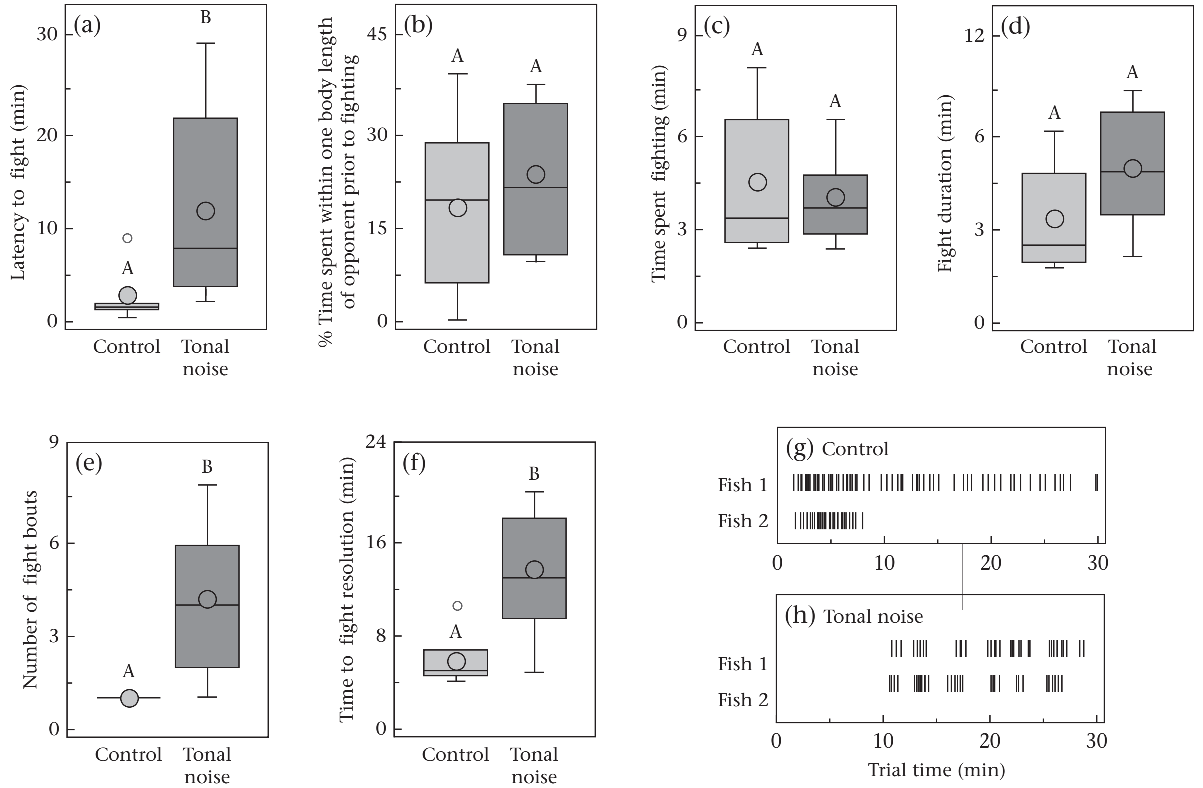

Figure 4. Effect of exposure to tonal noise and control conditions on male (a) latency to begin fighting (30 min maximum if no fight occurred), (b) percentage of time spent performing mutual assessment prior to fighting (i.e. time within one body length of opponent), (c) time spent fighting (i.e. cumulative bout duration), (d) fight duration (fight time and interbout interval), (e) number of fighting bouts and (f) time to fight resolution. (g–h) Representative raster plots of individual aggressive behaviours (black vertical lines) demonstrates differences in fight structure between sound conditions. Different letters indicate statistical significance at $P < 0.05$. $N = 7$ control trials, $N = 9$ noise trials (a, b), $N = 7$ noise trials with fights (c–f). Boxes extend to the furthest data points within the 25th/75th percentiles, and whiskers extend to the furthest data points within 1.5 the interquartile range. Outliers (beyond 1.5 the interquartile range) are designated by open circles and are not reflective of statistical outliers. Data median is represented by a solid line and data mean by a filled circle.

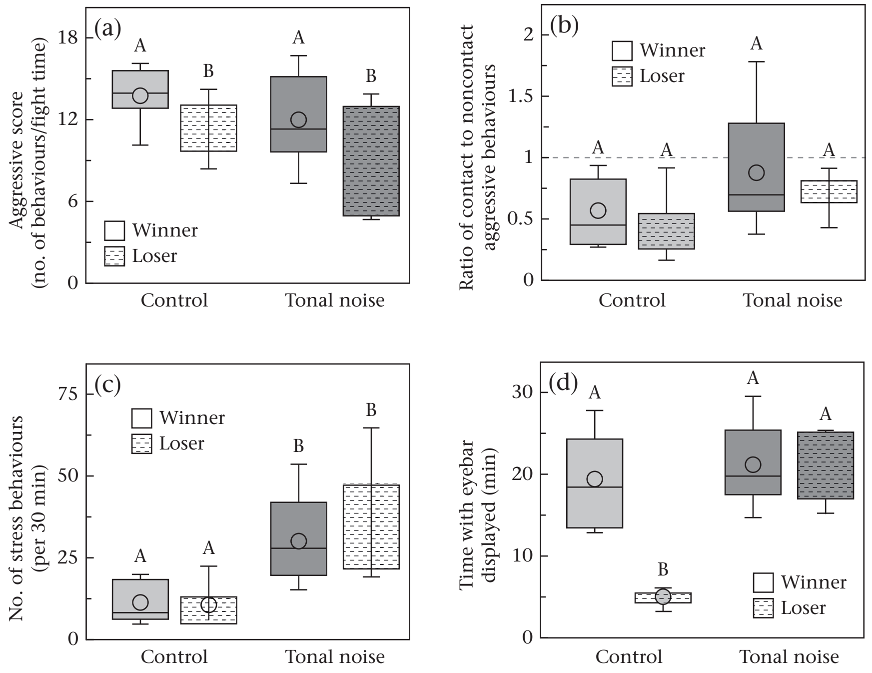

Figure 5. Effect of exposure to tonal noise and control conditions on male (a) aggressive scores (number of aggressive behaviours per fight minute), (b) use of contact (e.g. bites, rams),/noncontact (e.g. chases, lateral displays) behaviours; dotted line at 1 represents equal use of contact and noncontact behaviours, (c) stress behaviours (i.e. fin flaring, vertical banding, freezing) and (d) time with their eyebar displayed. Different letters indicate statistical significance at $P < 0.05$. $N = 7$ control fish per group, $N = 9$ noise fish per group. Box plot description as in Fig. 4.

noisy trials (2 behaviours: $t_{10} = 6.067$, $P < 0.001$; 3 behaviours: $t_{10} = 4.271$, $P = 0.002$; 4+ behaviours: $t_{10} = 2.304$, $P = 0.044$).

In addition to changes in courtship behaviours, males exposed to tonal noise performed aggressive behaviours towards the back wall (behind which the speaker was housed) or other tank objects (i.e. airstone, filter). No control males performed these displaced aggressive behaviours to the back wall, but all noise-exposed males did (Mann–Whitney U test: $U = 3.00$, $N_1 = N_2 = 6$, $P = 0.015$; Fig. 6f). However, stereotypical male aggressive behaviours directed at the female (bites, chases) did not differ between the two groups ($U = 14$, $N_1 = N_2 = 6$, $P = 0.589$), and these behaviours could be considered as part of the early courtship behavioural repertoire rather than aggressive. We used a hydrophone in the experimental tank to record male courtship sounds. While courtship sounds were easily identified in normal circumstances, we were unable to identify any courtship sounds audibly or visibly (from spectrogram) from recordings that occurred during the tonal noise condition.

Females were less responsive to male courtship behaviours when tonal noise was present. Female positive responses to male behaviours (i.e. following them or orienting towards them) was lower during noisy conditions (Student's t test: $t_{10} = 5.018$, $P < 0.001$; Fig. 7a). Females positively responded to ~50% (48.719 ± 7.901%) of male courtship events in control trials, but this was reduced to less than 10% (6.833 ± 2.676%) during tonal noise. Females also entered the pot less often during noise ($t_{10} = 2.292$, $P = 0.045$; Fig. 7b), but spent a similar amount of time in the shelter ($t_{10} = -0.584$, $P = 0.572$; Fig. 7c). This was because females often entered the pot near the beginning of the noise trials and stayed there, instead of revisiting multiple times throughout the trial. Noise-exposed females spent more time at the front wall of the tank (as far from the speaker as possible) than control females (Mann–Whitney U test: $U = 5.5$, $N_1 = N_2 = 6$, $P = 0.041$; Fig. 7d).

Circling behaviours (no egg laying) of the male–female pair occurred in all control trials (Fig. 8a). However, only 67% (4 of 6) of noise trials contained circling. In addition, spawning occurred in 67% (4 of 6) of control trials but only in 1 (17%) of the tonal noise trials. Circling behaviours always preceded spawning behaviours. The latency to initiate circling was longer during tonal noise trials compared to control trials (Student's t test: $t_{10} = 2.593$, $P = 0.029$; Fig. 8b). In trials where circling and/or spawning occurred, the number of circling/spawning events ($t_{10} = 1.739$, $P = 0.113$; Fig. 8c) and the time spent circling/spawning did not differ between the sound conditions ($t_{10} = 0.232$, $P = 0.823$; Fig. 8d).

Frequency-dependent Impacts of Tonal Noise on Behaviours

We investigated the impact of tone frequency on social and stress behaviours. Frequencies were binned into two low-frequency ranges (<200 Hz, 200–500 Hz), a middle frequency range (500–1000 Hz) and a high frequency range (>1000 Hz; Fig. 9a). Over 60% of stress behaviours were performed during high-frequency tones, and this was significantly higher than the percentage of stress behaviours in lower frequencies (ANOVA: $F_{3,68} = 179.990$, $P < 0.001$; Fig. 9b, see Table 2 for post hoc statistics). Aggressive ($F_{3,56} = 0.349$, $P = 0.790$) and displaced aggressive behaviours ($F_{3,20} = 0.283$, $P = 0.837$) were performed equally across all frequencies (Fig. 9c, d). Reproductive behaviours (male courtship displays, female affiliative behaviours) were performed equally in tones below 1000 Hz, but fish were less likely to perform reproductive behaviours during high frequencies (Fig. 9e, f; male: $F_{3,20} = 8.312$, $P = 0.002$; female: $F_{3,16} = 8.009$, $P = 0.003$; Table 2). There was no frequency-dependent effect on when circling and spawning bouts were initiated ($F_{3,16} = 2.865$, $P = 0.081$; Fig. 9g), although, on average, they were performed only 16% of the time during tones above 1000 Hz, compared to 28–29% in response to the lower-frequency tones.

Tonal Noise Exposure Impairs Gravid Female Hearing Capabilities

Under normal conditions, gravid females typically have the best hearing sensitivity between 200 and 300 Hz, which corresponds to peak frequencies of male courtship sounds (Maruska et al., 2012;

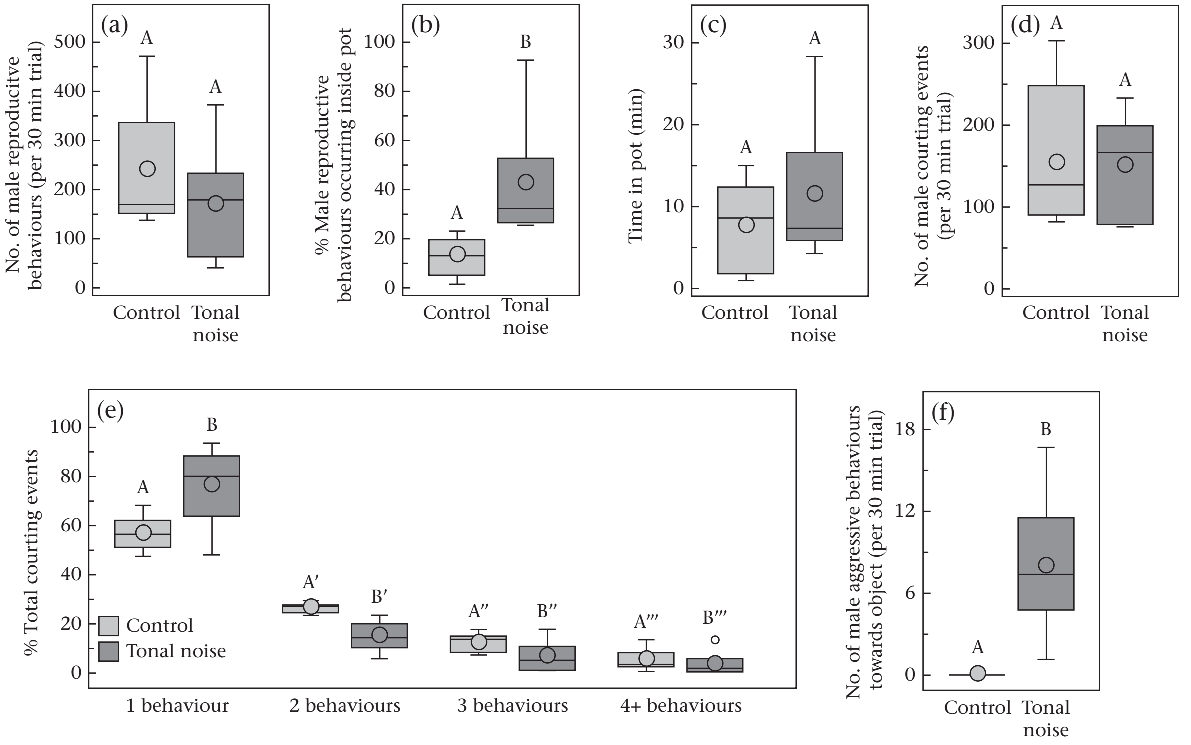

Figure 6. Effect of exposure to tonal noise and control conditions on male (a) reproductive behaviours, (b) reproductive behaviours inside the spawning shelter, (c) time in the pot, (d) number of courting events per 30 min trial, (e) percentage of total courting events and (f) number of aggressive behaviours (i.e. biting, frontal threats) towards tank objects, such as the airstone and speaker wall. Different letters indicate statistical significance at $P < 0.05$. $N = 6$ for all. Box plot description as in Fig. 4.

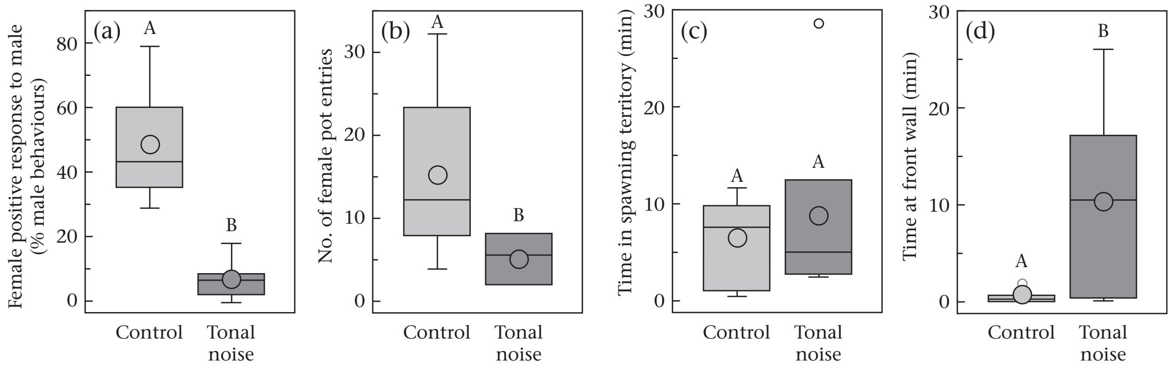

Figure 7. Effect of exposure to tonal noise and control conditions on female (a) positive responses to male courtship behaviours, (b) entries into the spawning shelter, (c) time in spawning territory and (d) time at the front wall of the experimental tank, far away from the speaker. Different letters indicate statistical significance at $P < 0.05$. $N = 6$ for all. See Methods for box plot descriptions.

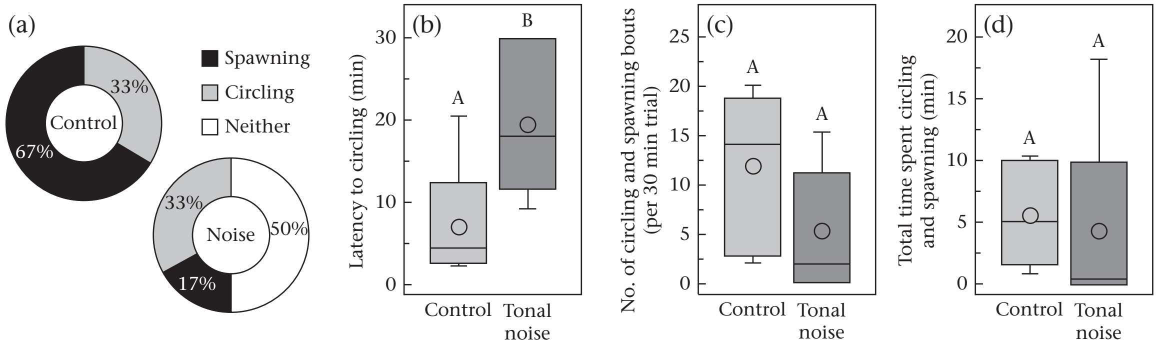

Figure 8. Effect of exposure to tonal noise and control conditions on (a) percentage of time spawning or circling, or neither, (b) latency to first circling bout (circling always preceded spawning), (c) number of circling/spawning bouts per trial and (d) total time engaged in circling/spawning. Different letters indicate statistical significance at $P < 0.05$. $N = 6$ for all. Box plot description as in Fig. 4.

Fig. 10). There was an overall effect of frequency (ANOVA: $F_{7,56} = 25.780$, $P < 0.001$), but not sound condition ($F_{1,56} = 3.727$, $P = 0.090$) on hearing thresholds recorded by AEPs in gravid females. However, the effect of sound condition was dependent on frequency ($F_{7,56} = 2.247$, $P = 0.044$). Noise-exposed gravid females had significantly higher thresholds (i.e. lower sensitivity) at 100 and 200 Hz compared to control females ($P = 0.003$, $P = 0.009$). There was no noise-induced threshold shift at 300, 400, 500, 600, 800 or 1000 Hz ($P > 0.05$ for all). Responses at low frequencies are likely a multimodal response, including both the auditory and lateral line systems. In the control AEP waveform traces, there was an overlay of higher-frequency responses over the low-frequency responses, suggesting a response of two different pathways in the brain (i.e. lateral line and inner ear). However, this higher-frequency response was not visible in AEP traces from noise-exposed fish.

DISCUSSION

Anthropogenic noise is pervasive in almost all aquatic and terrestrial environments and can have severe detrimental impacts on site-attached animals that are unlikely to leave their territory even in unfavourable conditions. Despite its crucial role in species persistence, there exists a paucity of information on how noise impacts social behaviours and communication. Using tonal noise to simulate a noisy environment, we found that while noise did not fully deter social interactions from occurring, territorial fights and circling/spawning were less likely to occur during noise. Tonal noise also changed how and where fish performed social behaviours. For example, instead of territorial fights occurring in a singular fight, they occurred in multiple bouts. During reproductive interactions, males performed more of their behaviours inside of the spawning shelter and females were less responsive to male courtship. Male behaviours also occurred as more singular events, instead of as a string of multiple behaviours. Behaviour strings may encode information differently than single behaviours, such that a male performing a string of four behaviours in close succession may

Table 2
Frequency-dependent effects of tones on social behaviours

Behaviour	Frequency bins		
	200–500 Hz	500–1000 Hz	>1000 Hz
Stress behaviours			
<200 Hz	0.089	0.625	**<0.001**
200–500 Hz		0.051	**<0.001**
500–1000 Hz			**<0.001**
Male reproductive			
<200 Hz	0.740	0.934	**0.002**
200–500 Hz		0.748	**0.018**
500–1000 Hz			**0.031**
Female reproductive			
<200 Hz	0.687	0.576	**0.009**
200–500 Hz		0.778	**0.036**
500–1000 Hz			**0.018**
Aggressive behaviours	No frequency-dependent effect		
Displaced aggression	No frequency-dependent effect		
Circling/spawning	No frequency-dependent effect		

Post hoc statistical results of how each frequency range impacts display of social behaviours. Bold values indicate statistical significance at $P < 0.05$.

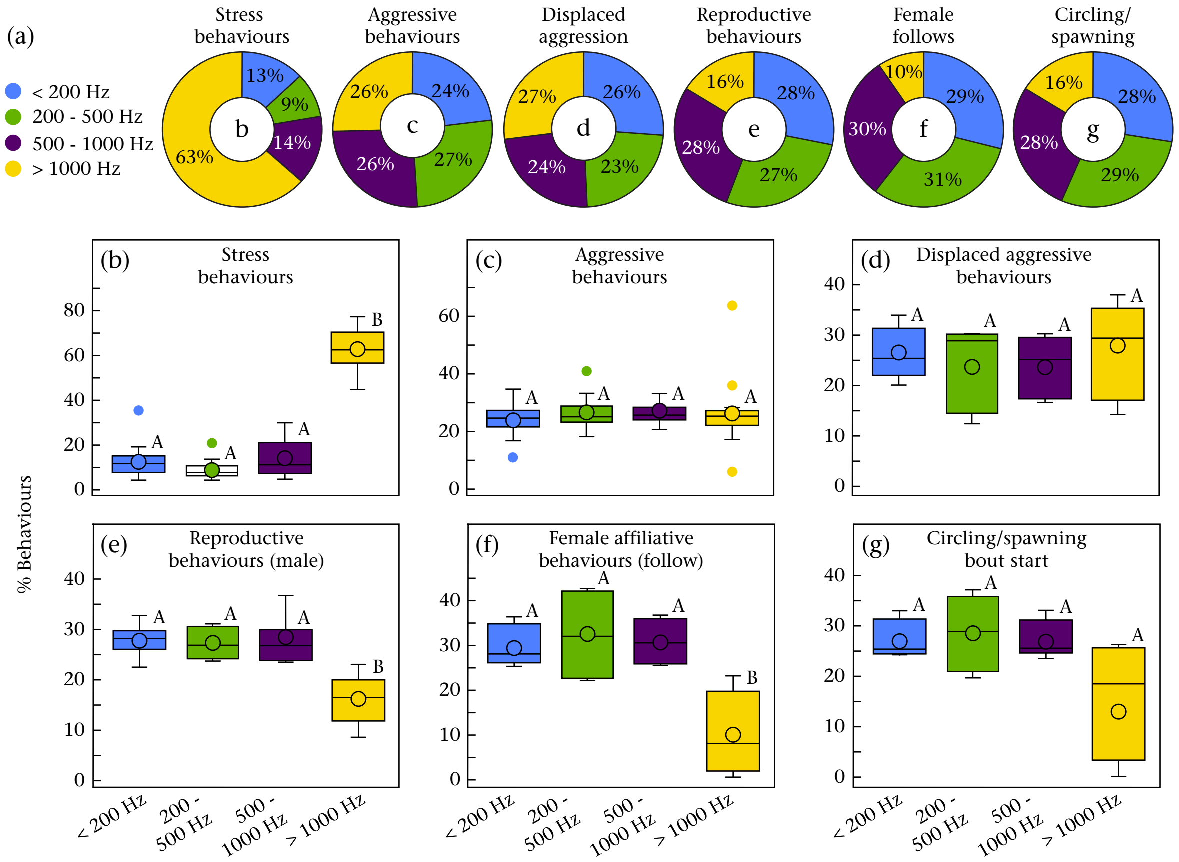

Figure 9. Frequency-dependent effects of tonal noise on the average percentage of (a, b) stress behaviours, (a, c) aggressive behaviours, (a, d) displaced aggressive behaviours, (a, e) male reproductive behaviours, (a, f) female affiliative behaviours ('follows') and (a, g) circling/spawning performed at <200 Hz, 200–500 Hz, 500–1000 Hz, and >1000 Hz. In (b–g), different letters indicate statistical significance at $P < 0.05$. $N = 5–6$ for all. Box plot description as in Fig. 4.

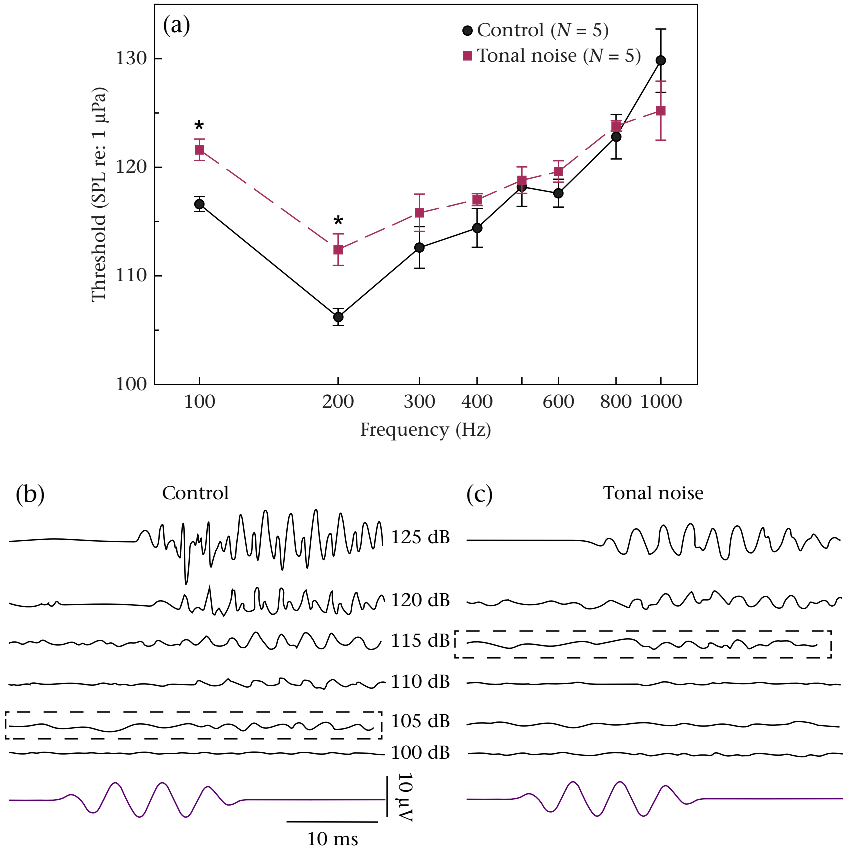

Figure 10. (a) Effect of exposure to tonal noise and control conditions on hearing thresholds of gravid females. ∗Indicates a significant difference within frequency between control and noise-exposed gravid females. Examples of auditory-evoked potential traces recorded from (b) control and (c) noise-exposed gravid females to 200 Hz stimuli (purple bottom trace). Threshold was determined as the lowest intensity that produced a repeatable waveform and the presence of an FFT peak at twice the stimulus frequency. For 200 Hz, threshold (dashed lines) was set to 105 dB and 115 dB for control and noise-exposed gravid females, respectively.

appear stronger or more fit than a male performing only one behaviour. In both territorial and reproductive interactions, fish performed more stress-like behaviours, such as freezing and flaring fins, hiding along the front wall of the tank and biting inanimate objects. Higher-frequency tones (>1000 Hz) had the greatest impact on behaviour, with stress behaviours performed more and reproductive behaviours performed less during high-frequency tones. Together, these data suggest that underwater tonal noise has negative impacts on social communication and behaviours in both territorial and reproductive contexts within a single fish species.

The ability to defend one's territory from rival males is vital to reproductive success. Like many territorial animals, male *A. burtoni* use their territory as a resource for reproduction, feeding and protection. Nonterritorial males are reproductively repressed and have little to no opportunity to spawn with females (Maruska, 2014). Importantly, males still defended their territory from rival males, even during tonal noise; however, they took longer to initiate a fight. This increased latency could relate to changes in cost–benefit analysis. For example, it is possible that the high background noise diminishes the quality of the territory (Brumm, 2004), making it less important to defend. The risks associated with a costly and dangerous territorial fight could outweigh the resource benefits of the territory. During aggressive interactions, *A. burtoni* males did not change the number or type of aggressive behaviours. In contrast, in the cooperatively breeding cichlid *Neolamprologus pulcher*, anthropogenic noise resulted in fewer digging (territory maintenance) behaviours (Bruintjes & Radford, 2013). Subordinate individuals also received more aggression from dominant fish, but the effects on aggression were both sex and context specific. Instead of changes to individual behaviours, we found that male–male fight structure was significantly altered during tonal noise. While we cannot tease apart the specific reason fish switched from fighting in a single fight to multiple bouts during tonal noise, one possibility is that the noise serves as a stressor and/or distraction. This is reflected in the higher number of stress behaviours, which were most commonly observed during the interbout interval time. Both stress behaviours and start of breaks in fighting corresponded to higher-frequency tones (<1000 Hz). The changes in fight behaviours observed, especially the increased time to fight resolution, can have negative impacts on antipredator behaviours. Engaging in a territorial fight makes an individual less aware of their surroundings, as does the types of behaviours being performed. South American cichlids, *Nannacara anomala*, were slower to detect approaching predators when engaged in contact behaviours compared with noncontact behaviours (Jakobsson, Brick, & Kullberg, 1995). In addition, anthropogenic noise can act as a further distraction and increase mortality due to predation (Simpson et al., 2016). Fathead minnows, *Pimephales promelas*, were less likely to respond to conspecific alarm (chemosensory) cues during noise (Hasan, Crane, Ferrari, & Chivers, 2018), and the Caribbean hermit crab, *Coenobita clypeatus*, allowed a simulated predator to get closer before noticing it (Chan et al., 2010). These noise-induced changes in antipredator behaviours can have major fitness consequences.

Anthropogenic noise is particularly pervasive in shallow shore areas, which unfortunately corresponds to where many territorial fishes live. Of the over 800 species of fishes that are known to produce sounds, most produce sounds during reproduction (Amorim, 2006). These sounds can encode vital information about the sender's sex, reproductive state, social status, size and motivation, but are typically only intended for close-range (<1 m) communication. During tonal noise trials, we were unable to distinguish male courtship sounds from background noise visibly or audibly from hydrophone recordings. This could be because we used small males, which produce quieter sounds, or because the males performed quivers more commonly inside the spawning shelter (i.e. farther away from the hydrophone), or because of the broadband nature of the sound. Because of these variables, we cannot determine whether male courtship sounds are masked by the additional tonal noise or whether males stopped performing courtship sounds during noise. Regardless of whether male sound production ceases or was masked by the noise, the outcome is likely the same; females would not have this male-generated acoustic information during courtship. We also found that noise-exposed gravid females had higher auditory thresholds, indicating worse hearing, at 100 and 200 Hz compared to control gravid females. This threshold shift corresponds to the dominant frequency component of male courtship sounds and the frequency range that gravid females are most sensitive to (Maruska et al., 2012). At low frequencies, AEPs are a multimodal response, such that both the auditory and lateral line systems contribute to low-frequency responses. Traces from control fish appear to have two different responses, corresponding to brain responses of the lateral line and auditory systems. However, the higher-frequency response to 200 Hz stimuli disappeared in noise-exposed females, suggesting an impairment of the lateral line system. Because the water movements associated with body quivers and tail waggles likely stimulate the female lateral line system (Butler & Maruska, 2016), this could indicate a breakdown in mechanosensory signalling during reproduction.

Male *A. burtoni* did not change the number of courtship behaviours performed (e.g. quivers, waggles), but they did change how and where they performed these behaviours. A sender must survey their environment and determine whether any factors may interfere with signal transmission and modify it as needed (Cole, 2013). To do this, senders may change the location, timing, type or sensory channel of the signal to maximize probability of detection. However, senders must also account for the energetic requirements of producing the signal, and if the costs outweigh the potential benefits, senders may choose not to engage in social communication at all. For example, it is the sender's responsibility to position their visual displays in a way that will maximize visibility to the receiver. In our reproductive context, this means dominant males are responsible for positioning their courtship in a way that increases the probability of female detection and response. In the natural environment and in our reproductive control trials, males often swim directly up to or in front of a female to produce a body quiver (with associated courtship sound) and tail-waggle. This close-range communication helps to ensure that females will detect and appropriately respond. However, when tonal noise was present during reproductive trials, males performed more behaviours inside of the spawning shelter instead of adjacent to females. When males do not display in front of the females, the females are unlikely to see and respond to these visual signals. Thus, by males simply changing the location of the courtship displays, they are likely removing or altering visual, mechanosensory and auditory signals intended to impress females.

When one sensory modality is disrupted, aside from ceasing communication altogether, two possible adjustments exist. First, animals can change how, when and where they produce their signals to maximize receiver detection and response. For acoustic communication in fishes, this is not always possible. Fish can change temporal aspects of their calls (i.e. produce sound during low-noise times) or increase the number and duration of calls, but physiological constraints inherent in the mechanisms of sound production typically prevent fish from being able to adjust the frequency or amplitude of their calls (Radford et al., 2014; but see Holt & Johnston, 2014; Luczkovich, Krahforst, Kelly, & Sprague, 2016). In contrast, birds, frogs and mammals are known to adjust the amplitude, pitch, repetition rate and duration of notes during abiotic noise (e.g. Grafe et al., 2012; Ríos-Chelén, Lee, & Patricelli, 2015). An alternative strategy to modulating the disrupted channel is to instead switch channels to a less disturbed one. These cross-modal changes due to noise are observed in several species of fishes. Noise had no effect on nest building in either the two-spotted goby, *Gobiusculus flavescens*, or painted goby, *Pomatoschistus pictus* (de Jong et al., 2018a). However, both species decreased the number of drumming behaviours but not the number of thumps. Interestingly, in two-spotted gobies, there was no change in visual displays, but painted goby males decreased their visual displays during noise. This demonstrates that, even in closely related species, noise can have different effects. While noise decreased the number of visual and acoustic displays by male painted gobies, it also changed the female's preference for visual and acoustic signals (de Jong, Amorim, Fonseca, & Heubel, 2018b). Under control conditions, a female's preference was predicted by the number of male acoustic displays. However, when noise was added, females instead relied on visual displays for mate choice. Similar to our results in the cichlid, painted gobies had decreased spawning rates during noise (de Jong et al., 2018a). Aquatic invertebrates such as cuttlefish (*Sepia officitialis*) also suffer from noise-induced effects across multiple sensory modalities (Kunc, Lyons, Sigwart, McLaughlin, & Houghton, 2014) by increasing their visual displays. Importantly, the authors of that study noted that these cross-modal changes in visual behaviours can help mitigate the negative impacts of noise but do not completely compensate. This is especially true in species that use nonredundant signalling in which signals in different sensory channels provide receivers with different types of information (Johnstone, 1996; Partan & Marler, 1999). Both male and female *A. burtoni* are known to contextually release their urine (containing putative pheromones) in the presence of threats or reproductive opportunities (Field & Maruska, 2017; Maruska & Fernald, 2012). Because this species can control when and where they release their urine, future studies should test for cross-modal impacts of noise on chemosensory signalling. Combined with our data, this highlights the importance of considering the natural multimodal nature of social interactions and possibility of cross-modal changes due to noise.

Cross-modal impacts of tonal noise were not restricted to reproductive contexts. Male *A. burtoni* spent more time displaying their eyebar during noisy trials. Males displaying an eyebar are behaviourally more likely to attack another male, and conversely, are more likely to be attacked (Leong, 1969). As such, visual display of the eyebar is an essential component of male–male aggressive interactions (Heiligenberg, Kramer, & Schulz, 1972). Under control conditions, both males displayed their eyebar at the beginning of the trial. As the fight progressed, the losing fish stopped displaying his eyebar while the winner maintained it for the duration of the trial. However, both the fight winner and loser spent equal time with the eyebar displayed during tonal noise, even after the conclusion of the fight. Eyebar 'on' is the default state (Muske & Fernald, 1987), so this increased display of the eyebar could relate to not turning the eyebar 'off' due to stress or other energetic demands. During periods of stress, males typically get vertical banding along their trunk and often have their eyebar displayed, but the eyebar was displayed in noise-exposed males even when vertical banding was absent. Although we are unable to determine whether the increase in eyebar displays is a by-product of stress or an intentional signal, it ultimately results in a similar outcome: an increased visual display of dominance. Perhaps this increased visual cue, even during nonfight times, could explain why fight structure was changed. Instead of turning their eyebar off at the conclusion of a fight, the eyebar remained on, leading to continued fighting and aggression between the two males.

Laboratory-based studies for examining the impacts of noise on fish have many limitations (Slabbekoorn, 2016). We used tonal noise instead of boat playback or other recordings of anthropogenic noise because the distortion that occurs in small tanks will render playbacks of real anthropogenic noise similarly unrealistic (Akamatsu et al., 2002) and because it allowed us to examine frequency-dependent impacts of tonal noise on behaviours. The use of tonal noise does not represent a naturalistic stimulus, and as such, any behavioural changes we observed, especially those that were frequency dependent, may not be extended to ecologically relevant sounds. However, this approach allowed us to determine that tones above 1000 Hz had the largest behavioural impact, which was not expected since *A. burtoni* have generally poor hearing at these frequencies (Maruska at el., 2012). In addition, spectrograms of the tonal noise playback suggest that the sound file produced a more broadband sound than intended. Visually, it is difficult to distinguish the different frequency components. Despite this, fish appear to be able to audibly distinguish at least the high-frequency range. This could possibly be due to the fact the discrimination capabilities of the auditory system are remarkably sensitive. The behavioural response to higher-frequency tones could be due to fish not being exposed naturally to this frequency range at volumes that they would be able to detect. While we slowly raised the volume on the amplifier so that there was not an abrupt onset of noise to cause a startle response, we cannot rule out the possibility that behavioural changes were due to stress or startle response to a novel stimulus. However, it is impossible to decouple stress effects related to noise from impacts of changes in the soundscape alone. We also had relatively small sample sizes, although the behavioural responses were robust and repeatable. Due to these limitations, one should refrain from extending conclusions here to responses that might occur in the wild under more naturalistic environmental conditions. Instead, future studies are needed that combine laboratory and field studies to fully understand how noise impacts fishes. Only by combining the controlled laboratory experiments with the more ecologically relevant field studies, will we be able to understand how noise impacts fish on multiple levels of biological organization (Popper & Hastings, 2009; Slabbekoorn, 2016; Williams et al., 2015).

Anthropogenic noise is a global pollutant and affects most aquatic and terrestrial ecosystems (Shannon et al., 2016). Changes to natural soundscapes are limiting communication space (Alves et al., 2016; Putland, Merchant, Farcas, & Radford, 2018; Slabbekoorn et al., 2010) and affect many life-history stages (Popper & Hastings, 2009; Radford et al., 2014; Shannon et al., 2016). While traditional studies on noise exposure focused on major organ damage, mortality and other dramatic impacts (for review see Popper & Hastings, 2009), recent research has focused on sublethal impacts of noise (e.g. foraging: Bracciali et al., 2012; Chan et al., 2010; McLaughlin et al., 2015; social behaviours: Bruintjes & Radford, 2013; development: Bruintjes & Radford, 2014; Nedelec et al., 2015; reproduction: de Jong et al., 2018a; communication: de Jong et al., 2018b; Luczkovich et al., 2016; Lugli et al., 2003). By examining these subtle changes in behaviour, physiology and communication due to noise exposure using well-controlled field and laboratory studies, we can identify earlier indicators of noise susceptibility (Graham & Cooke, 2008; Kunc, McLaughlin, & Schmidt, 2016; Slabbekoorn, 2016). These subtle changes could be more important for management and conservation efforts across a wide range of species moving forward.

Changes in social communication can have dramatic impacts on sexual selection and mate choice (Laiolo, 2010; Van der Sluijs et al., 2011). As evidenced in gobies, noise in one sensory modality can shift the relative importance of signals in other channels and even drive loss of certain signals (de Jong et al., 2018b). When testing for anthropogenic effects on social behaviours and communication, we should focus on all three components of communication: the production of the signal (behaviour), transmission of the signal (environment) and the receiver's physiology (ability to detect the signal) and behavioural response. More studies are needed to examine noise-induced impacts on signal production (timing, location) before we can fully understand the determinantal impacts that anthropogenic noise can have on animals. All together, these studies highlight the species, sex and context-specific effects of anthropogenic noise on a social, territorial and relatively site-attached fish.

Data Availability

All data sets will be made available upon reasonable request.

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Conflict of Interest

We declare no competing or financial interests.

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