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Aggressive Acoustic Behavior in Yasuhikotakia Modesta: Does the Lombard Effect Hold Water?

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AGGRESSIVE ACOUSTIC BEHAVIOR IN *YASUHIKOTAKIA MODESTA*:
DOES THE LOMBARD EFFECT HOLD WATER?

A Capstone Experience/Thesis Project

Presented in Partial Fulfillment of the Requirements for

The Degree

Bachelor of Science with

Honors College Graduate Distinction at Western Kentucky University

By

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2012

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ABSTRACT

The Lombard effect is the automatic and involuntary change in the intensity of vocalizations in the presence of background noise in order to maintain a constant signal to noise ratio. While this phenomenon is commonly found in vocalizing terrestrial vertebrates, it had not previously been examined in aquatic vertebrates such as fishes. This experiment tests the presence of the Lombard effect in the red-finned loach, *Yasuhikotakia modesta*, which make two types of sounds: butting and clicking. I recorded three pairs of *Y. modesta* during aggressive interactions over territory and compared the sounds produced in silence with sounds produced in the presence of background noise (approximately 120 dB re 1 μ Pa). An increase of approximately seven dB was found for maximum click amplitudes in the presence of background noise compared to those in quiet control conditions. Butting sounds did not change significantly in response to background noise. Aggressive behaviors that accompanied the sounds were also categorized, and were labeled as: chasing, circling, ramming, intimidation, lateral displaying, biting, and defending behaviors. This is the first study that presents evidence that the Lombard effect may be present in fishes.

Keywords: Lombard Effect, *Yasuhikotakia modesta*, Aggressive, Behaviors, Fish, Communication

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CHAPTER 1

INTRODUCTION

Hearing and Acoustic Signaling in Fishes

Many people carry the misconception that sound plays little part in the lives of fishes; however, the fish inner ear works very similarly to those of terrestrial vertebrates, relying on the movement of specialized hair cells originating from the vibration of other structures (Fay & Popper 2000). In mammals, sound vibrations are first carried through the membrane of the eardrum and then through three small bones of the middle ear; the movement of these bones cause movement in the fluid in the cochlea, around the organ of Corti, which bends and stimulates the hair cells. In fish, sound waves travel through the bodies of fish, whose tissues are of similar to the density the water. Structures of differing density (such as dense otoliths or the air-filled swim bladder) move out of sync with the fish's body in response to sound waves, which causes the bending and stimulation of the hair cells. While all fish species that have been studied possess the ability to hear (Kasumyan 2005), some species produce their own sounds which can be used as communicative signals. In fact, the largest diversity of sound-production mechanisms in vertebrates can be found in fishes (Ladich & Fine 2006).

Fishes cannot vocalize the same way that humans or other terrestrial vertebrates do; they do not have the lungs required to force air over vocal chords, but rather different

taxonomic lineages have evolved many different mechanisms to produce sound. Fish can generate sounds through a drumming muscle apparatus and stridulatory, pneumatic, and plucking mechanisms (Ladich & Fine 2006). The drumming muscle refers to the muscles around the swim bladder of a fish; when these muscles contract, they vibrate the air-filled swim bladder to produce a low-frequency sound like a drum (Ladich 2000). The drumming apparatus is the sound production mechanism of characids, searobins, toadfishes, and drums (Ladich 2000). Stridulatory mechanisms, or stridulation, involves the grinding of skeletal elements like teeth or bone (Ladich & Fine 2006) and generates sound in sculpins, catfishes, and cichlids (Ladich 2000). Pneumatic mechanisms produce sounds by pushing air from either the swim bladder or gastrointestinal tract through small ducts; this mechanism is found in cobitid fishes and clupeids (Wilson et al. 2004). Fish that produce sound through a plucking mechanism, such as croaking gouramis, pull and release on tendons like those found in the pectoral fins (Ladich 2000). Sounds can also be produced unintentionally by fish, such as the hydrodynamic sounds produced by swimming, the sounds produced when feeding, and sounds made by contact with surrounding objects; these sounds are not thought to act as communication (Ladich & Fine 2006).

Threats to Acoustic Signaling in Fishes

Human activity in the oceans and waterways has been creating noise of increasing intensity as technology has evolved, and many scientists are beginning to wonder how this anthropogenic sound will affect fishes. Over the past 50 years, boats and ships have contributed to an increase in low-frequency background noise in the ocean by 32-fold

(Malakoff 2010). While much attention has been given in the past to how loud sounds affect aquatic mammals, and this has been examined even more extensively in terrestrial organisms such as birds, it has taken the scientific community longer to recognize the importance of hearing and vocalization to many species of fishes (Slabbekoorn et al. 2010). While the ocean and freshwater waterways are far from silent – even without the added noise of human activities such as drilling, boating, and construction – the relatively sudden and often long-lasting anthropogenic sound that is added to underwater environments could be detrimental to fishes, as many fish species rely on sound production for finding mates (Verzijden 2010) or territorial defense (Ladich 1997). Scientists are becoming concerned with how fish will cope with the noise, or if they are even capable of doing so. One natural mechanism that could help vocalizing fish cope with loud anthropogenic noise is the Lombard effect.

The Lombard Effect

The Lombard effect, named after Etienne Lombard who first described it in 1911, is the automatic and involuntary change in the intensity of vocalizations in the presence of background noise in order to maintain a constant signal to noise ratio (Lau 2008). The automatic change in the amplitude of produced sounds in the presence of background noise aids the communication of vocalizing animals by increasing their vocalizations over noise that could mask quieter calls (Brumm & Todt 2002).

The Lombard effect has been described in several different types of vocalizing animals, but has been most commonly studied in birds and primates. The effect has been described in both territorial songbirds such as the nightingale, *Luscinia megarhynchos*,

and non-territorial birds such as the Japanese quail, *Coturnix coturnix japonica*, and the zebra finch, *Taeniopygia guttata* (Brumm & Todt 2002). These birds do not maximize the amplitude of their songs every time they sing, but sing at an adjusted amplitude depending on the amount of background noise (Brumm 2004). In a study of the Lombard effect in primates, macaques were found to selectively alter the amplitude of their vocalizations in the presence of sound that impaired their ability to hear themselves (Sinnott et al. 1975). Numerous studies have also shown that this phenomenon is evident in humans (Brown & Brandt 1972; Summers et al. 1988; Junqua 1996; Lane & Tranel 1971; Lau 2008). Apart from birds and primates, frogs have also been recorded as having a tendency to increase the amplitude of their calls in the presence of masking background sound (Lopez et al. 1988).

Research Purpose and Implications

No studies of the Lombard effect had been previously conducted on fishes, although many different methods of fish sound production have been described (Ladich 2000). Because of the very different nature of the sound production in fishes compared to terrestrial vertebrates, it is currently unknown whether the Lombard effect evolved in fishes or if it was a separate event in terrestrial vertebrates. Testing for the Lombard effect in fish has the potential to answer several biological questions. In an evolutionary biology context, it is currently unknown if this effect evolved alongside hearing – which is believed to have first evolved in fishes (Manley & Clack 2004) – and sound production in fish, or if it evolved later in terrestrial vertebrates. In the context of conservation biology, many questions concerning how loud sound affects fishes have been raised in

response to the increasing anthropogenic noise in the oceans since many fish rely on sound for mating and territorial defense (Slabbekoorn et al. 2010), and it is unclear how masking background noise might impact fish behaviors, survival, and reproductive fitness. The purpose of my research was to test for the Lombard effect in *Yasuhikotakia modesta* – the red-finned loach.

Test Subjects

For this project, I chose *Y. modesta*, a species of freshwater loach that is fairly common in the aquarium trade, because their sound production was described to be relatively simple to initiate without complications due to mating or hormone requirements, making it potentially easy for researchers to manipulate the timing of sound production (Raffinger & Ladich 2009). Since it is impossible to determine the sex of *Y. modesta* without the aid of dissection, the sex of all fish in this experiment was unknown; however, both male and female *Y. modesta* are very territorial and defend their territory by producing two different types of sounds while engaging in aggressive behaviors (Raffinger & Ladich 2009).

The first type of sound these fish can produce is called “clicking” and consists of short, loud clicks with a dominant frequency that ranges from 90 to 330 Hz and an average Sound Pressure Level (SPL) of 102 dB re 1 μ Pa (Raffinger & Ladich 2009). The exact mechanism for click production is still unknown, but it is hypothesized that the sounds originate in the stridulatory movement of the pharyngeal jaws – a second pair of jaws within the throat used for crushing the carapaces of prey, such as mollusks (Raffinger & Ladich 2009). The second type of sound is referred to as a “butting” sound,

and is made when one fish hits the other with a part of its body, usually the head. The average SPL and frequency range of the butting sounds was previously quantified to be 106 dB re 1 μ Pa and from 80 to 330 Hz, respectively (Raffinger & Ladich 2009). The butting sounds are thought to be unintentional sounds. By analyzing the volume of the two types of sounds produced by *Y. modesta* first in quiet conditions and then in the presence of background noise, I was able to discern how loud background noise affects the sound production of these fish. Not only did testing for the presence of the Lombard effect in *Y. modesta* provide clues as to how some vocalizing fish might cope with loud background noise, but it also provides evidence that the Lombard effect may have evolved alongside hearing and vocalization in fishes, and not as a separate event in terrestrial vertebrates.

CHAPTER 2

METHODS

Tank Setup

Six *Y. modesta*, ranging in size from 5.65 cm to 7.21 cm total length (TL), were maintained in three different aquaria: a first holding tank containing 151 L of water, a 38 L experimental tank, and a second 151 L holding tank. The holding tanks contained a charcoal filter, water heater, a substrate of sand and gravel, and artificial plants and plastic PVC pipes to act as territory and shelters for the fish. The test subjects were kept in the first holding tank until they were to be placed in the experimental tank in pairs. The smaller experimental tank was divided by an opaque, removable Plexiglas wall that separated the tank into two halves. Each half contained a submersible charcoal filter, a water heater, and a PVC pipe (5 cm diameter, 10 cm length) that acted as territory and shelter for the fish that occupied that side of the tank. To reduce unwanted background noise, the experimental tank was surrounded on four sides by a box-like chamber lined with soundproof foam. The front of the sound-proof box was left open for observation. Following an experimental trial, the fish were removed from the experimental tank, and were placed in the second holding tank to keep used and unused fish separated. All tanks were kept at approximately 25°C and on a 12:12 light-dark cycle.

Trials and Treatment Conditions

Before each experimental trial, a pair of *Y. modesta* was taken from the holding tank and placed in the experimental tank, each fish occupying its own side. They were allowed to acclimate to the tank for at least two months; this was because the fish would become too startled to defend their territory during the experiments until they had fully explored the tank and settled into their PVC pipe shelters. After this acclimation period, the experimental trial began. In these trials, quiet conditions acted as the control and noisy conditions acted as the treatment. Each pair's trial consisted of two recording sessions over the course of two days. On the first day, the recording sessions consisted of quiet conditions for five minutes, followed by five minutes of white noise. During the second day's recording session, the quiet and noise conditions were reversed with five minutes of noise followed by five minutes of quiet. This reverse of conditions was to account for the possibility that the fish may produce fewer or quieter sounds once they became tired, or other time-dependent experimental artifacts.

Recording Session Procedures and Equipment

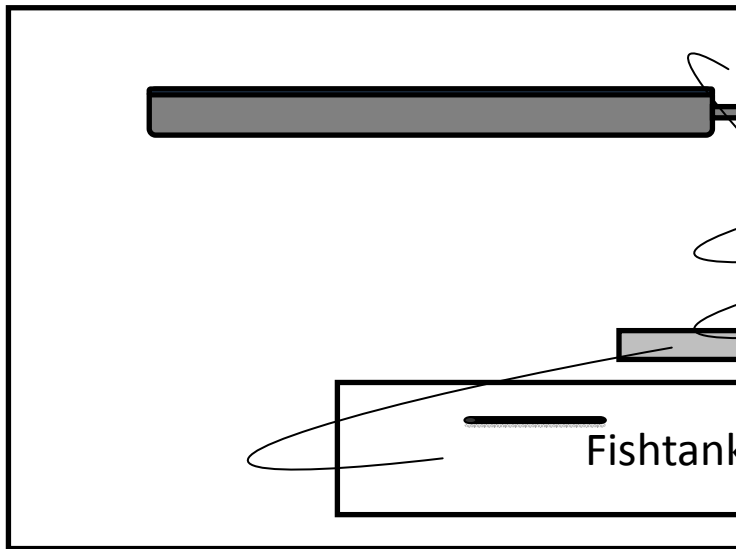
Behavioral interactions were recorded for three pairs of *Y. modesta* in a repeated-measures design. Pair one consisted of fish that both had a total length (TL) of 6.93 cm, pair two consisted of fish that were 5.65 cm and 6.21 cm TL, and pair three consisted of fish that were 7.21 cm and 5.91 cm TL. Fifteen minutes before recording, the filtration systems and heaters were turned off and removed from the water, and a GRAS 8103 hydrophone was placed in the water centered above the middle of the PVC pipe on the left side of the tank. Two minutes before recording, the opaque divider was lifted and the

fish from the right side of the tank was coaxed to move to the left side, which forced it to invade the other's territory and initiated territorial dispute. The opaque divider was returned to its normal position, and an underwater speaker (University Sound UW-30) was placed on the right side of the tank behind the replaced barrier to keep the fish from hiding behind or under the speaker. During noisy conditions, continuous white noise was played at a Sound Pressure Level (SPL) of approximately 120 dB re 1 μ Pa through the underwater speaker (approximately 14.5 cm from the hydrophone) fed through an Audiosource amplifier. This SPL was chosen because, during preliminary recordings, it was found to be above the mean click volume but still under the volume of the louder clicks recorded. During quiet conditions, the underwater speaker was turned off with all other conditions being the same as during noisy conditions. After the ten minute recording session, the underwater speaker and hydrophone were removed, and the fish were returned to their original sides.

For each session, fish behavior and sounds were recorded simultaneously (Figure 2.1). Sound was recorded through the hydrophone and sent through a PE & ISOTRON Signal Conditioner and Amplifier and a Quest Scientific Humbug, which reduced electrical noise. The signal was then sent through a PEAVEY PV6 mixer, which reduced electrical noise further and split the sound so that it could be recorded simultaneously on a computer and on video via a Sony digital video recorder.

Analysis

Videos of the sessions were used to determine the behaviors that the fish were engaged in while sounds were made and what type of sound each one was (butting or



clicking). Recorded sounds were labeled as butting sounds when the sound was made, or labeled as clicking sounds when the sound was made. The individual sounds were analyzed using sound analysis software (Raven Pro, Version 1.4), and the maximum amplitude was recorded for each sound. This maximum amplitude was calculated with the equation $20(\text{Log}_{10}A) + C = \text{SPL}$, where A is the maximum amplitude of the recorded sound and C is the maximum amplitude of the sound in the environment. Analysis of variance (ANOVA), using SYSTAT version 12 statistical software, was used to test the effects of background white noise on the maximum SPL of the sounds. For each pair, the twenty loudest clicking sounds from both conditions were used in analysis (except for pair three, which produced no clicking sounds in noisy conditions) to account for the potential effect of background white noise. Butting sounds were generally less common, so all of the loudest

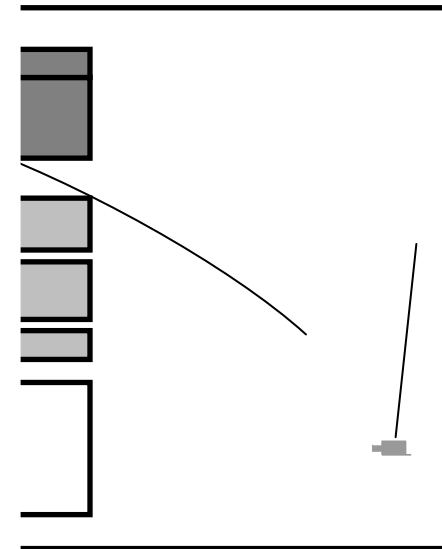


Figure 2.1. Technical equipment. A = amplifier; B = Humbug sound conditioner; C = PEAVY PV6 sound mixer.

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butting sounds up to twenty were used from each condition. This means that there was an even number of clicking sounds for each condition of each pair, but usually unequal butting sounds since usually fewer were made. Behaviors that the fish engaged in while producing sounds were recorded and analyzed to see if the Lombard effect was present during some behaviors more than others.

Test for Additive Effects of Sound

A technical test was performed to ensure that any increase in amplitude of fish sounds was not a result of an additive effect of the white noise background sound on *Y. modesta* sounds. During the test, two underwater speakers and a hydrophone were placed in the experimental tank. One speaker played white noise at 120 dB, while the other played digitally-produced man-made clicks at 129 dB. A one-minute recording of repeated pure clicks separated by five seconds was recorded, followed by a one-minute recording of clicks and white noise. The SPL of both recordings were analyzed to determine if any change in the clicks was caused due to a potential additive effect of the white noise. No additive effect was found (Figure 2.2).

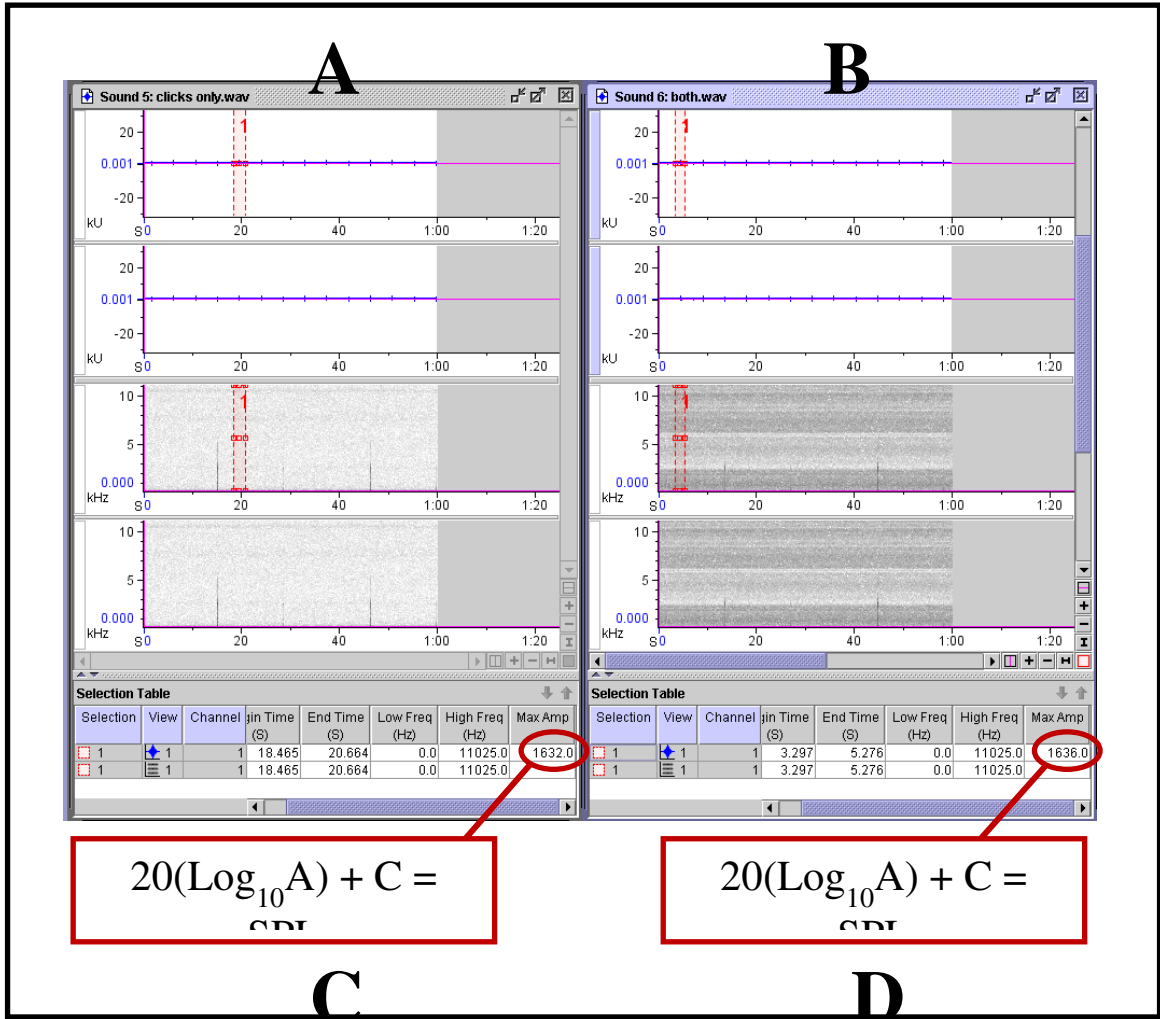


Figure 2.2. Technical test results. Oscillograms and spectrograms for digital clicks only (A) and digital clicks in the presence of 120 dB re 1 μPa white noise (B). SPL computation for clicks only (C) and clicks with white noise (D).

CHAPTER 3

RESULTS

Sound Analysis

Evidence in support of the presence of the Lombard effect in *Y. modesta* was found. All three pairs of *Y. modesta* exhibited a significant ($P < 0.001$) increase in the SPL of their clicks in the presence of background noise (Figure 3.1). Pairs one, two, and three exhibited mean click SPLs that were 9, 4, and 7 dB greater under noisy conditions than quiet conditions, respectively. Across all pairs, there was a mean difference of 6.6 dB in the click SPL in the presence of white noise. Due to the logarithmic nature of decibels, this is an increase in sound amplitude of approximately 460%. No significant change was observed in the SPL of the butting sounds.

Behavior Analysis

Ladich had previously described three aggressive behaviors for *Y. modesta* (Raffinger & Ladich, 2009), which consisted of: lateral (parallel) displaying, during which the two fish swim side by side and fan their fins to make themselves seem larger; chasing, where one fish chases the other around the tank; and circling, where the two fish spin in a tight circle while following the other's tail (Figure 3.2). Along with these

previously documented behaviors, four more behaviors were recorded: defending, where

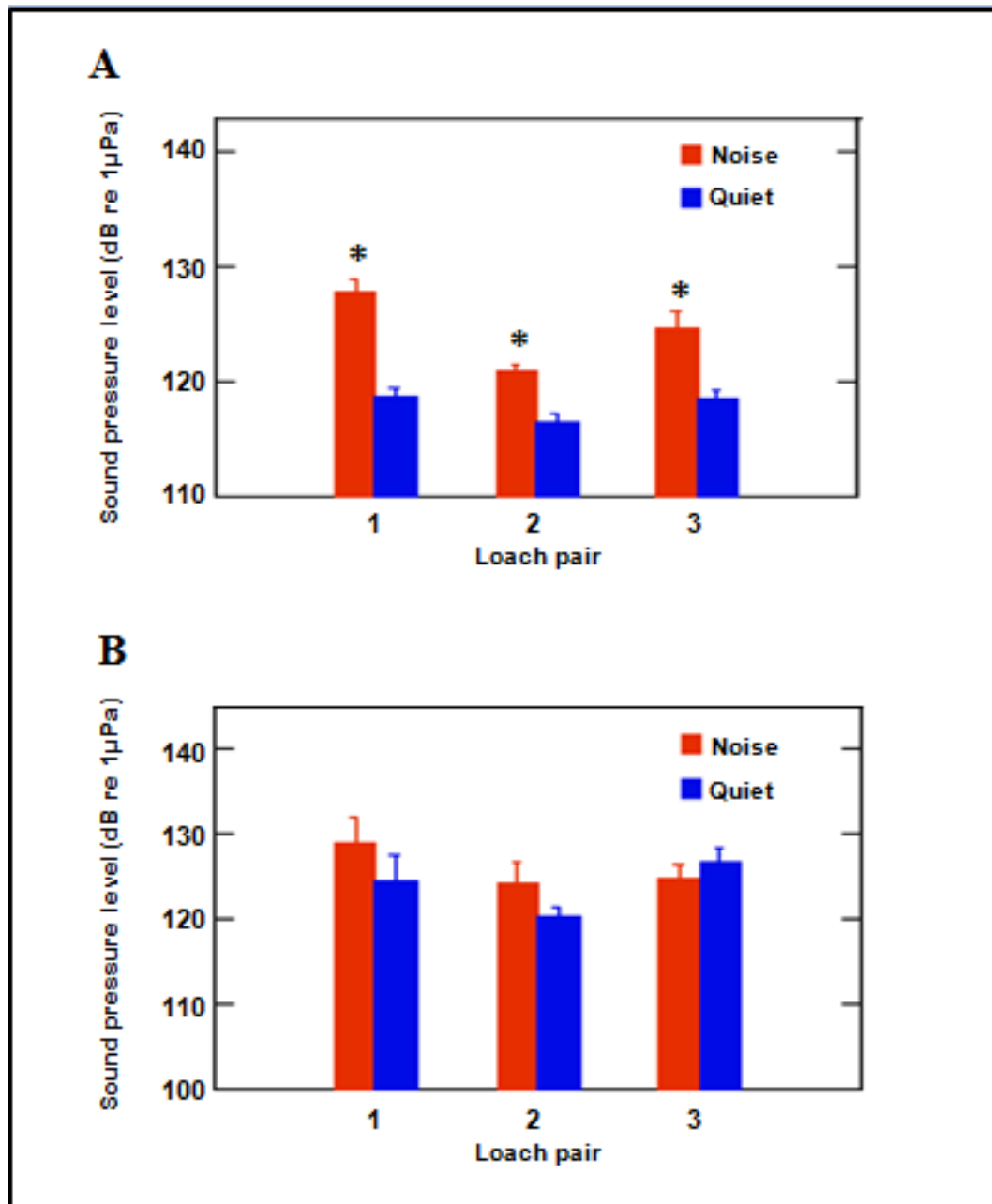


Figure 3.1. Mean (\pm SE) sound pressure level (dB re 1 μ Pa) of clicks (A) and butting sounds (B) under quiet (blue) or white noise (red) conditions. * P < 0.001.

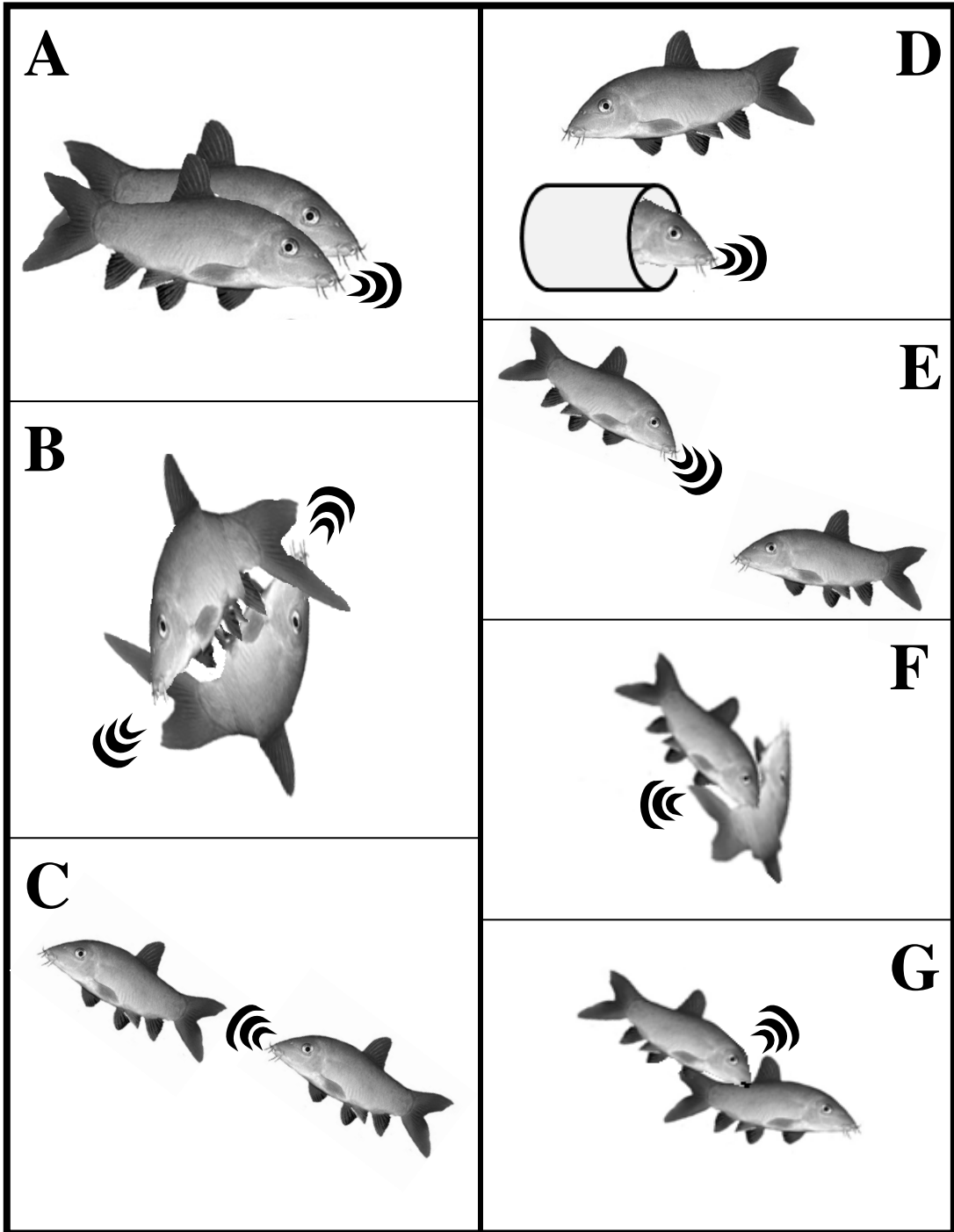


Figure 3.2. Illustration of aggressive behaviors of *Y. modesta*. Behaviors described by Raffinger & Ladich (2009) = lateral display (A), circling (B), chasing (C). New behaviors = defending (D), intimidation (E), ramming (F), biting (G).

one fish holds its position within the shelter and clicks to the other as it swims outside; ramming, where one fish swims quickly at the other fish and uses the momentum of its body to push the other into the substrate; intimidation, where one fish clicks at the other from a distance, perhaps as a potential warning; and biting, where one fish grips the other with its mouth (Figure 3.2).

Aggressive behaviors were analyzed to see what behaviors produced clicks or butting sounds and how often the fish made sounds while engaging in these behaviors (Figure 3.3). Intimidation, biting, and defending were three behaviors that only produced clicks, whereas ramming was a behavior that only produced butting sounds. Ramming was also the most common behavior that produced butting sounds. The vast majority of vocalizations were produced during circling behavior. There were 45 clicking sounds that were the result of circling behavior, which was 20 more than intimidation, the second most occurring click-producing behavior. There were fewer butting sounds produced during circling. Chasing behavior resulted in more butting sounds than clicks, but lateral display produced the same number of clicks and butting sounds.

Aggressive behaviors were also analyzed to see how the sound production during each individual behavior changed as a result of background noise (Figure 3.4). While there were no significant patterns in the butting sounds, four of the six behaviors that produced clicking sounds experienced a significant increase in the SPL of the

vocalizations: circling ($P < 0.001$), defending ($P < 0.013$), intimidation ($P < 0.002$), and lateral display ($P < 0.001$).

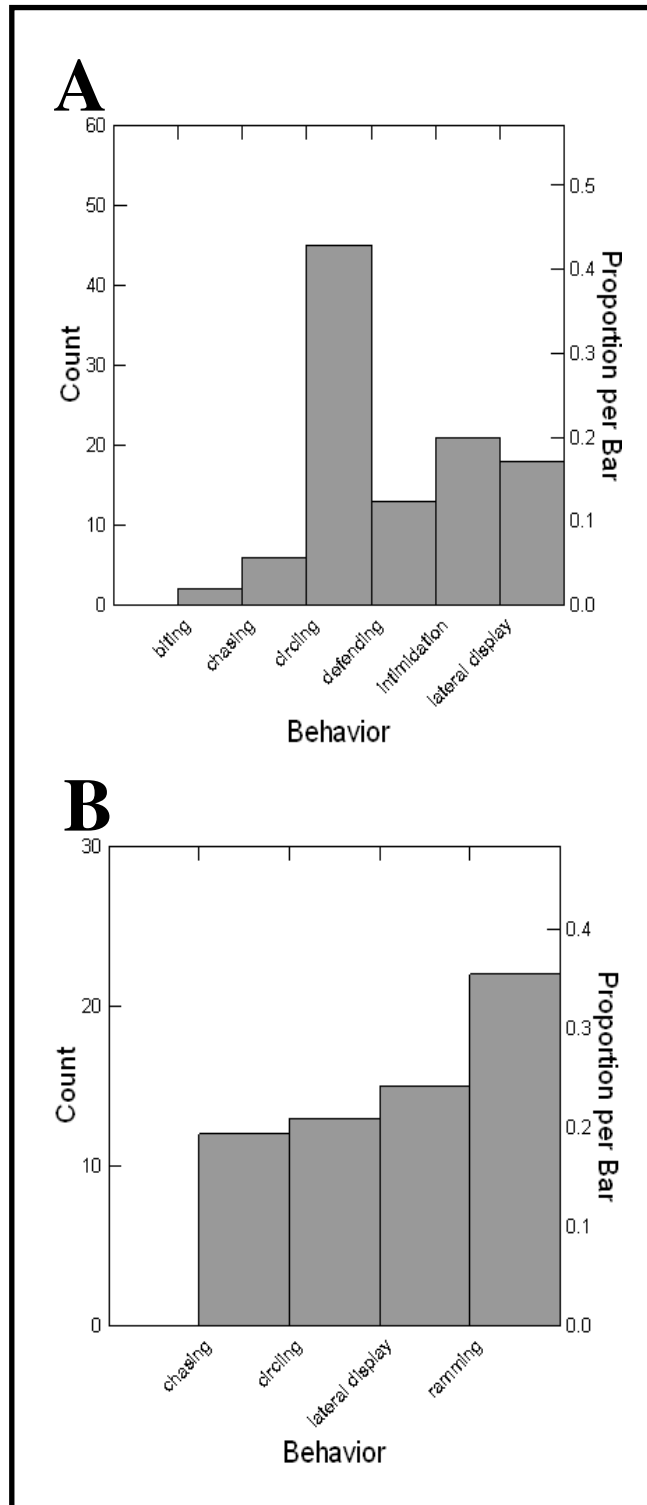


Figure 3.3. Histogram of click-producing behaviors (A) and butting sound producing behaviors (B).

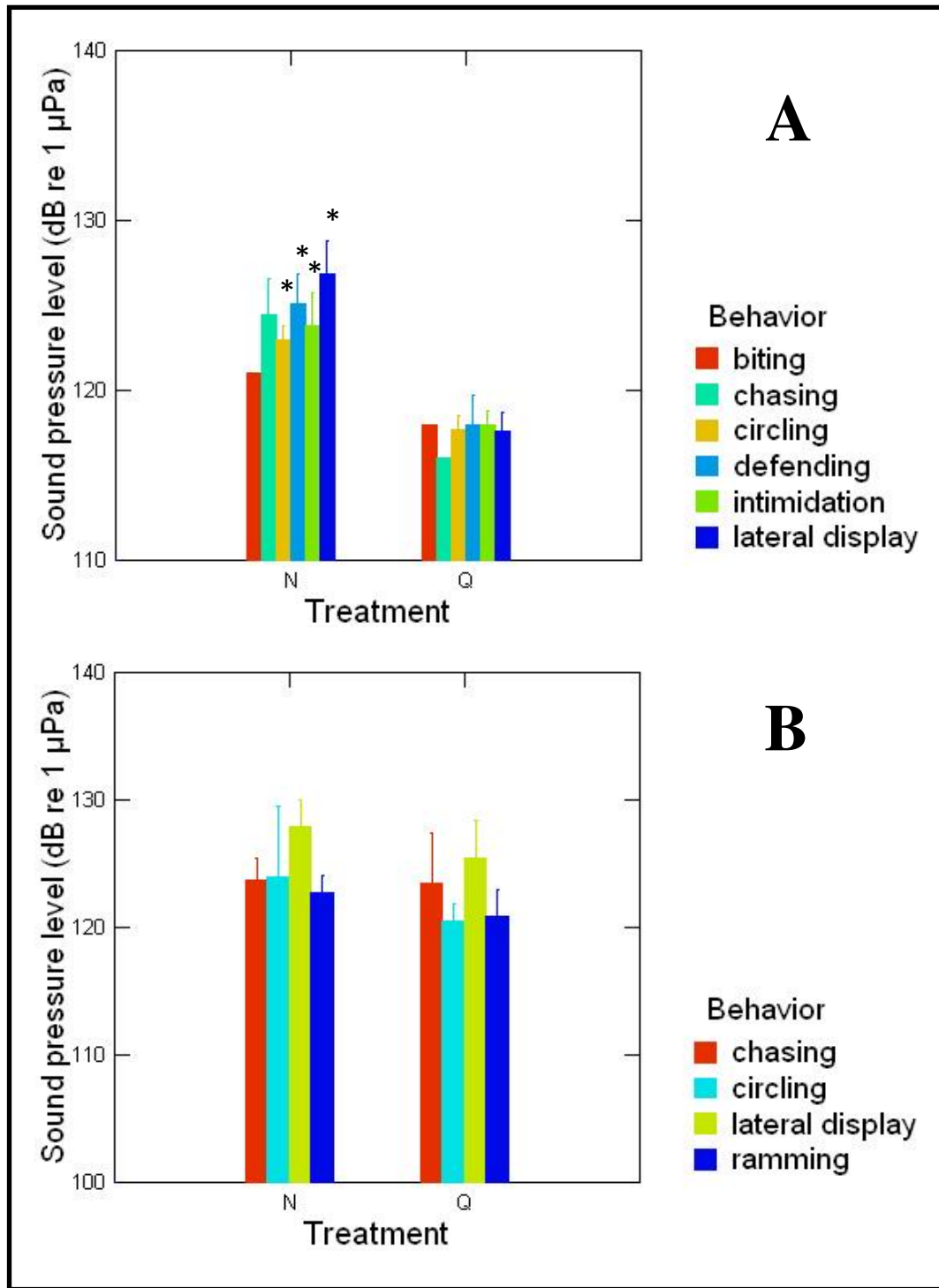


Figure 3.4. Aggressive behavior mean (\pm SE) sound pressure level for clicks (A) and butting sounds (B). * $P < 0.05$

CHAPTER 4

DISCUSSION

The Lombard Effect and Sound Production in Fishes

The significant increase in the amplitude of *Y. modesta* clicking sounds is the first evidence of the Lombard effect occurring in fishes. This means that fish may possess the ability to appropriately modulate their communication in different background noise levels, rather than being completely masked. How this modulation may occur in *Y. modesta* clicks is unclear, but it is hypothesized that these clicks are produced by stridulating the pharyngeal jaws, as *Y. modesta* possesses a set of pharyngeal jaws (Raffinger & Ladich 2009) and a number of other fish taxa produce sound via pharyngeal jaw stridulation, such as cichlids (Ladich & Bass 1998), some species of weakfish (Connaughton & Taylor 1995), and damselfish (Rice & Lobel 2004). It is reasonable to postulate that increased pharyngeal jaw muscle contractions could lead to increased amplitude of click production, but future experiments using electromyography during *Y. modesta* sound production would be needed to test this hypothesis.

Several experiments have shown that different fish species are able to detect acoustic signals in the presence of ambient masking noise with varying success (Wysocki et al. 2007), but hearing-sensitive fish require the intensity of acoustic signals to increase drastically in the presence of masking background noise – up to 50 dB louder in the case

of carp (Amoser & Ladich 2005). Some fish species are known to combat masking in flowing bodies of water by occupying “acoustic niches” where vocalization frequencies fall into a noise window that is outside the strongest ambient noise frequencies (Wysoki et al. 2007). An example of this is the European goby, *Padogobius martensii*, which produces its peak frequencies in the frequency range of weakest acoustic power of the surrounding ambient noise (Lugli & Fine 2003). However, my data shows that the Lombard effect may provide fishes like *Y. modesta* with a means of communication over masking background noise, such as anthropogenic noise.

The lack of a significant change in the SPL of butting sounds suggests that these sounds cannot be controlled enough to exhibit the Lombard effect. It is likely that the volume of *Y. modesta*'s butting sounds depends on how hard the fish hits against the other and how the opponent reacts. It is also likely that butting sounds are unintentional and do not serve as acoustic communication, such as the sounds made by fish while they are feeding, swimming, or breathing (Ladich & Fine 2006). However, this lack of significance could also be explained by some of the small sample sizes of the butting sounds.

The Lombard Effect and Size Variation

There was significant variation in the amount of increase in the mean click SPL between the three pairs. This may be explained by the difference in the size (total length) of the fish. The first pair consisted of two fish that were 6.93 cm TL and exhibited the highest mean click SPL in the presence of white noise. The second pair consisted of fish that were 5.65 cm and 6.21 TL and exhibited the lowest mean click SPL. The third pair

consisted of fish that were 7.21 cm and 5.91 cm TL fish and exhibited a mean click SPL that was between pair one and pair two. While these size differences were not intentional and were not the focus of this experiment, this trend could suggest that larger fish exhibit more of a Lombard effect than smaller fish. Previous research on sound production in fish of differing sizes has revealed that vocalization amplitude is positively correlated with body length and mass in cichlids (Bertucci et al. 2012); therefore it is likely that larger members of *Y. modesta* are able to produce louder sounds in the presence of masking background noise. However, more research is needed before any conclusions can be made.

Data Comparison to Previous Experiments

In this experiment, the mean SPL of both clicks and butting sounds are much higher than those previously recorded. Raffinger and Ladich (2009) recorded mean SPL of *Y. modesta* clicks of 102 dB re 1 μ Pa, and mean SPL of butting sounds of 106 dB re 1 μ Pa, while the sounds recorded in this experiment ranged from approximately 115 to 137 dB re 1 μ Pa. There are several potential reasons for this difference. Raffinger and Ladich (2009) used juvenile *Y. modesta* that were between 5.3 cm and 6.3 cm TL. The smaller-sized juveniles may not have been able to produce the louder sounds seen in my experiment. This variance in SPL between experiments may also be due to the fact that the data for this experiment was limited to the maximum sounds produced in each condition to account for potential masking. Many sounds closer to 110 dB were recorded in quiet conditions (below which the sounds were masked by electrical noise), but they were not included in the top twenty sounds. The difference in SPL measurements

between different laboratories could also be related to the use of different sound recording equipment and calibration in the two experiments.

In order to compare the background sound-induced increase in the mean SPL of *Y. modesta* clicks to the data that already exists for the Lombard effect in terrestrial vertebrates, it must be understood that sound waves behave differently in water than they do in air. Because of the higher molecular density and acoustic impedance of water compared to air, sound travels five times faster and farther in water than it does in air, and it travels at higher amplitudes (Slabbekoorn et al. 2010). In air, SPL is measured with reference to 20 μ Pa, and aquatic SPL is measured with reference to 1 μ Pa (Slabbekoorn et al. 2010). Because of this, a 25.5 dB correction is required to convert aquatic dB to airborne dB; this is done by subtracting 25.5 dB from aquatic measurements or adding 25.5 dB to airborne measurements (Slabbekoorn et al. 2010).

Brumm and Todt (2002) described an increase in the SPL of nightingale's vocalizations by about 5-10 dB, depending on the specimen, when background noise was increased from 35 dB to 75 dB (a 40 dB difference). After correcting for the aquatic SPL, the airborne equivalent to the white noise played for *Y. modesta* was 94.5 dB and the quiet conditions were 84.5 dB, and there was an overall increase in *Y. modesta* click SPL ranging from 4-9 dB, depending on the pair. This comparison suggests that *Y. modesta* had a comparable response to the nightingales', but in reaction to a much smaller change in background noise; however, the 84.5 dB re 20 μ Pa background noise in quiet conditions was mostly caused by an electrical hum that the hydrophone picked up, and would not have been detected by *Y. modesta*'s auditory system. If so, the fish and birds in these experiments could have very similar responses to background noise due to

the Lombard effect.

Variation in Significance of Click Behaviors

Only four of the six behaviors that produced clicking sounds exhibited a significant increase in mean SPL when in noisy conditions: circling, defending, intimidation, and lateral display. Chasing and biting behaviors did not exhibit a significant increase. This could indicate that some clicks are more important to *Y. modesta* acoustic signaling than others. The clicks that accompany biting behavior may be unintentional, caused by the scraping of the fish's pharyngeal teeth as the fish bites down. While it is less likely that clicks that occur during chasing are unintentional, it is possible that the fish devotes less energy to the click because more energy is needed for the actual chase. While circling also involves movement, the movement is confined to a small space around the opponent. Also, circling occurs when both fish are actively trying to gain dominance, whereas chasing involves one fish fleeing from the other. Therefore, a fish that is chasing another might not need to devote as much energy to making a threatening vocalization as a fish competing for dominance. Alternatively, it is possible that the lack of significance resulted from chasing behavior clicks occurring at different distances from the hydrophone, whereas circling behavior tended to occur in the same areas of the tank.

Future Research

More experiments need to be done to be able to say that all or most sound producing fish exhibit the Lombard effect; however, from this data we can conclude that

members of *Y. modesta* exhibit the Lombard effect. The next step in this research will be to perform this experiment on other species of vocalizing fish. Many different species that utilize a variety of different types of sound production mechanisms must be examined before it can be known whether all vocalizing fish exhibit the Lombard effect, or if it arose independently in only a few lineages.

It is likely that the Lombard effect will only be present in vocalizing fish that have a great amount of control of the sound producing mechanism and the muscles associated with it. While it is likely that stridulatory mechanisms that use skeletal muscle can be consciously controlled, there is some uncertainty whether or not fish that utilize a drumming apparatus are able to adequately control the strength of the muscle contractions over the swim bladder. Some research indicates that swim bladder sound amplitudes are not affected by size and do not significantly change in amplitude (Parmentier et al. 2011), while other research indicates that fish like *Ophidion rochei* have very complicated swim bladder musculature and produce sounds that grow in amplitude as they are produced in rapid succession (Parmentier et al. 2010). Since different fish species that use drumming mechanisms possess different musculatures surrounding the swim bladder, many different species of drumming fish will have to be examined in future studies. If most vocalizing fish species are found to exhibit the Lombard effect despite the diversity of their sound production mechanisms, this would be strong evidence to support the hypothesis that the evolution of the Lombard effect first occurred in fishes.

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