2014

A Not-So-Silent Spring: The Impacts of Traffic Noise on Call Features of The Bloody Bay Poison Frog (Mannophryne olmonae)

Catherine G. Clemmens
The College of Wooster, cgclemmens@gmail.com

Recommended Citation

Clemmens, Catherine G., "A Not-So-Silent Spring: The Impacts of Traffic Noise on Call Features of The Bloody Bay Poison Frog (Mannophryne olmonae)" (2014). *Senior Independent Study Theses.* Paper 5783.
https://openworks.wooster.edu/independentstudy/5783

A NOT-SO-SILENT SPRING:
THE IMPACTS OF TRAFFIC NOISE ON CALL FEATURES OF THE BLOODY BAY POISON FROG (*MANNOPHRYNE OLMONAE)*

DEPARTMENT OF BIOLOGY

INDEPENDENT STUDY THESIS

Catherine Grace Clemmens

Adviser: Richard Lehtinen

Submitted in Partial Fulfillment of the Requirement for
Independent Study Thesis in Biology at the
COLLEGE OF WOOSTER 2014

TABLE OF CONTENTS

ABSTRACT

Anthropogenic noise has been shown to alter the behavior of a wide array of creatures in the animal kingdom. One of the most significant types of anthropogenic noise is traffic noise, and research in this area has only recently begun to emerge. I investigated the effect of traffic noise on ten parameters of the call of the Bloody Bay Poison Frog (*Mannophryne olmonae*) by analyzing field recordings from 35 sites in eastern Tobago, West Indies. Statistically significant increases in high frequency, change in frequency, as well as a significant decrease in the inter-pulse interval were found at sites with high levels of traffic noise. There were also non-significant, but noteworthy trends in both pulse duration and upper harmonics. There were longer pulses, and greater amounts of upper harmonics at low noise sites than high noise sites. This study's findings suggest that *M.olmonae*'s vocal modifications are likely an attempt to escape from the low-frequency masking of traffic noise. As frogs and toads warn us of potential consequences of human caused environmental degradation before they manifest in other species, they are often considered to be good indicator species. Consequently, this study may forewarn us of future effects of traffic noise for other acoustically communicating species.

INTRODUCTION

Throughout our history, humanity has accomplished countless amazing feats. This saga, from our very beginnings, to the Neolithic revolution when we learned to farm, to the moon landing and the recent discovery of the Higgs Boson particle, has occurred in just 100,000 years. While that may seem like a long time, the Earth has supported life forms for at least 3.7 billion years (Stearns and Hoekstra, 2005). In other words, if a 24-hour clock encapsulated the entire history of the earth, humans would not even appear until the last few seconds before midnight. Yet, in those few seconds we have literally changed the face of the earth. Some of our alterations are initially imperceptible, such as climate change. It wasn't until 2001 that it was widely agreed that the buildup of CO_2 and other greenhouse gases emitted by humans are causing climate change and all its effects (e.g. melting polar ice caps, extreme seasonal changes in temperature and precipitation, altered species distributions and ocean acidification) (Boykoff and Boykoff, 2004; Intergovernmental Panel on Climate Change, 2007; Walther et al., 2002). Other human changes are easily perceptible, such as habitat loss to make way for construction. Whether the construction is for the Great Wall of China or today's housing, industry, or attractions like theme parks and malls, we have paved over the natural environment to make way for a new human terrain. This study focuses on an inevitable byproduct of our construction: roads.

Roads directly impact the ecology of approximately 15-20% of the land in the United States. The area over which the ecological effects of a road extends into the surrounding environment is termed the road effect zone (Forman and Alexander, 1998).

The three primary problems that roads create for wildlife are direct mortality, habitat fragmentation and habitat loss; all three of which reduce population sizes (Jaeger et al., 2005). It has been estimated that one million vertebrates are killed on roads every day in America (Forman and Alexander, 1998). Habitat fragmentation- the division of an organism's natural environment into smaller isolated segments - often blocks the natural movement of organisms. It can force organisms to face problems such as migration blockages, population subdivision, inbreeding, resource depression, and loss of genetic variation (Jaeger et al., 2005; Kaiser and Hammers, 2009; Keller and Largiader, 2003; Parris et al., 2009). Other effects on the surrounding environment by nearby roads include runoff, decreasing biodiversity, alteration of the landscape, disruption of ecological routines, and habitat fragmentation. All of these create a plethora of problems. Runoff alone causes increased erosion, reduced percolation, lower aquifer regeneration rates, increased flood levels, and aquatic degradation (Forman and Alexander, 1998). However, some consequences of roads are less studied than others. One in particular is anthropogenic noise pollution. Much like the CO_2 emanating from our cars, anthropogenic noise pollution is invisible and until recently it has been relatively overlooked.

Behavioral Effects of Anthropogenic Noise

The cars we drive produce a variety of sounds. The friction of each tire as it turns on the pavement creates noise, as do the engine and speakers. In general a sound wave is produced by a disturbance that displaces molecules of the air creating a chain reaction of vibrations; these vibrations eventually reach a tympanic membrane and are translated by electric signals to the brain as a sound (Forrest, 1994; Narins et al., 2006). However, a sound cannot travel indefinitely. As a sound propagates from its starting point, the vibrations are spread over a wide area and the energy dissipates (Forrest, 1994). Many factors can affect how a sound propagates. Different environments allow certain frequencies to travel farther than others. Surfaces such as trees or the ground can reflect and absorb sonic vibrations, and other noises in the environment may mask certain sounds. Different amplitudes and frequencies of the sound also impact its capacity to travel through an environment. The amplitude of a sound is the height of the sound wave, which represents the maximum displacement of air particles from their mean position. The frequency is how often the oscillations of the sound wave vibrations occur (Everest, 2009; Hartmann, 2013; Parker, 2009). These are commonly known as “loudness” and “pitch” respectively, although neither are perfect synonyms (Pijanowski et al., 2011). Anthropogenic noise generally has a low frequency and high amplitude. Urban environments in particular contain anthropogenic noise that mostly occurs at frequencies less than 4 kHz (Pijanowski et al., 2011).

Anthropogenic noise has been shown to alter the behavior in a wide array of creatures within the animal kingdom. A study by R.J Windle et al. demonstrated that captive Sprague-Dawley rats previously exposed to high intensity and periodic noise had averse reactions such as stress and decreased reproductive output (Windle et al., 1997) On the other side of the size spectrum, Beluga whales have shown signs of disturbance such as diving, veering away and other apparent short-term reactions to helicopter noise (Patenaude et al., 2002). There is also a correlation between U.S. Navy sonar use and mass strandings -live and dead- in many whale species. When examined, the whales' tissues show "bubble-like lesions" believed to be caused by decompression sickness due to atypical behavioral reactions to the sonar (Parsons et al., 2008). Both wolves and elk have significantly elevated stress hormone levels directly correlating to the proximity of off-road vehicles, such as snowmobiles (Creel et al., 2002). A study by Schaub et al. demonstrated that greater mouse eared bats, avoid foraging in areas subject to traffic noise. Even domestic chickens that have been living on our farms for hundreds of years show increased behavioral stress and decreased immune function after being exposed to traffic noise (Schaub et al., 2008). Although signs of stress in animals such as rats, whales, wolves, elk, bats and birds have all been studied, the research on the effects of anthropogenic noise on animal *communication* has recently become a burgeoning field. Birds, because of their ubiquity in developed areas, make especially good study subjects and, fittingly, the bulk of research on anthropogenic noise impacts has focused on avian communication.

A common theme among studies of birdcalls and urban noise is masking (Dowling et al., 2012; Slabbekoorn and Peet, 2003; Wood et al., 2006). Masking occurs when the background noise reduces the active distance of an organism's acoustic emissions. A vocalization's active distance is the distance over which it can be detected by a conspecific (Parris et al., 2009). Birds have several strategies to reduce the effects of masking caused by anthropogenic noise. There is evidence indicating that birds undergo periods of vocal plasticity in which they have the ability to change characteristics of their songs (Patricelli and Blickley, 2006). In a study by Dowling et al. (2012) the Gray Catbird and Northern Cardinal - both species with a normally low song frequency - increased the minimum frequency of their calls in response to anthropogenic noise. Greater effects of urban noise have been found in species that normally have a lower song frequency, this may be because in contrast to the natural acoustics of an environment, anthropogenic noise pollution typically occurs at high amplitudes and low frequencies (Dowling et al., 2012; Francis et al., 2009). Other birds, such as the Common Nightingale, increase the amplitude of their song, known as the Lombard effect, in areas of higher anthropogenic noise (Brumm and Todt, 2002). Some species show plasticity for both the frequency and amplitude of their songs. This was seen in the Song Sparrow which increased the frequencies of the lower notes, and decreased the amplitude of the notes in the lower frequency ranges of their songs (Wood et al., 2006). However, vocal plasticity is not the only means by which birds have avoided the masking of anthropogenic noise. Many have been shown to change the timing of their songs. They select and sing songs that are not masked by their environment (Patricelli and Blickley, 2006; Warren et al., 2006). Masking is also a concern for other highly vocal species. Frog (anuran) species in particular rely heavily on their calls, and thus may be exceptionally sensitive to anthropogenic noise.

Effects of Anthropogenic Noise on Frog Vocalization

One of the most significant types of anthropogenic noise is traffic noise. Scientists have only recently begun to detect the possible impacts of traffic related noise on frog calls. Recently, a study was conducted using a mathematical model to predict the active distance that an advertisement call will travel in urban areas compared to rural areas. The overarching result was that all species of frogs are anticipated to face significant acoustic interference in urban environments; specifically an 81-94% reduction in the active distance of the call for frogs measuring a 15-95 mm snout vent length (Parris, 2013). High levels of traffic noise (noise exceeding 60 dB) have been shown to significantly lower call rates of green frogs (*Rana clamitans*), northern leopard frogs (*Rana pipiens*), and gray tree frogs (*Hyla versicolor*). It has also been shown to affect the call amplitude of green frogs and the call frequency of both green and northern leopard frogs (Cunnington and Fahrig, 2010). A study performed by Bee & Swanson demonstrated that noise from nearby traffic interfered with female grey tree frogs (*Hyla chrysoscelis*) perception of male advertisement calls (Bee and Swanson, 2007). Traffic has also been shown to interfere in brown tree frog (*Litoria ewingii*) vocalizations to the extent that the frequency alterations in the calls were clearly detectable by conspecific females (Parris et al., 2009). An increase in call rate of *Rana taipehensis* vocalizations has also been correlated with airplane flyovers, motorcycles as well as experimental playbacks of anthropogenic noise (Sun and Narins, 2005).

Much as with songbirds, there is evidence that some species of frogs may shift the timing of their calls to avoid coinciding with high levels of noise pollution and other species have exhibited the Lombard effect (Warren et al., 2006). A study on male Woodhouse’s toads (*Bufo woodhousei*) found that attributes of the calls varied significantly near highway noise. Males from sites with greater traffic noise exposure had a significantly higher frequency, reduced call rate, longer call, greater duration between calls, and a lower reaction rate to normal calls (Barrass, 1985). The increased frequency and longer call duration are both hypothesized to be noise avoidance mechanisms (Barrass, 1985). These mechanisms may have carried over from exposure to more natural sources of masking. Although traffic noise is a major concern now, it certainly was not the first time frogs had to cope with masking.

Before traffic noise existed, frogs had to overcome at least one natural form of masking: the calls of conspecifics. This is common in breeding choruses, and there are times when many different species of frogs may be calling and masking the vocalizations of other species if the frequencies are similar (Wollerman, 1999). Frogs apparently use similar techniques to overcome both traffic noise and interspecific sources of masking. Research has revealed that some species of frogs have changed their calls through shifts in frequency, amplitude, call rate and inter-pulse intervals (Given, 1999; Grafe et al., 2012; Kaiser and Hammers, 2009; Lopez et al., 1988; Penna and Hamilton-West, 2007; Schwartz, 1993; Sullivan, 1985). In some species of frogs a phenomenon called upper harmonics is seen, and may be used as a method of reducing masking. Upper harmonics can be defined as harmonics (notes that mirror the original pulse and occur at the same time point as the pulse) with lower amplitudes and higher frequencies than the original pulse. With all the mechanisms frogs use to overcome the masking of conspecifics it may seem that anthropogenic noise pollution is not exceptionally detrimental. However, many of the aforementioned mechanisms have serious consequences.

In all species there are tradeoffs between the allocation of resources to reproduction and survival. This is because resources and energy available to organisms are limited. Calling is very likely to be the most energetically costly action male frogs will engage in during their lifetime (Cunnington and Fahrig, 2010). Frogs that alter their vocalizations in order to increase their call's transmittance across an environment will use more of their energy stores. To counteract this they will need to either increase their foraging time and/or decrease their calling time (Kaiser et al., 2011). An increase in foraging may expose them to more predators, and definitely limits their time spent in the breeding chorus. It has been shown that chorus tenure (the number of nights a frog calls at a particular breeding site) is negatively associated with increases in call amplitude (Kaiser et al., 2011). This decrease in chorus tenure decreases male fitness. However, this was studied in reaction to increased conspecific calling, not in response to anthropogenic noise. It remains to be seen whether frogs will similarly compensate for anthropogenic noise (Kaiser et al., 2011).

Why Should We Care? The Importance of Calling for Frogs

Calling is crucial for the majority of frog species' survival. Calls contain information about a frog's calling site, species identity, and reproductive status (Parris et al., 2009). Calls are used predominately by males to attract mates and declare territory, while females prevailingly utilize male calls to assess potential mates (Warren et al., 2006). There are two major concerns about anthropogenic noise pollution; the first is the possibility of restricting the distribution of animals that have a low noise tolerance, the second is the possible detrimental impact on the reproductive success of species forced to reside in environments highly exposed to anthropogenic noise (Warren et al., 2006).

A study by Barrass focused on the direct effects of highway traffic noise on both anuran vocalizations and reproduction. Barrass found that male location as well as the amount of male aggregation varied significantly when in close proximity to traffic noise. The spacing of calling males and the extent of their aggregation deviated significantly from the normal spacing patterns away from high noise areas (Barrass, 1985). Additionally, when highway traffic noise was played back in a secluded environment the male frogs dispersed, disbanding from their calling aggregations and individually relocating further away from their conspecifics (Barrass, 1985).

It is now known that females use the spatial distribution of male vocalizations to enhance the detection of male calls (Wollerman, 1999). A study by Schwartz and Gerhardt found that female American green tree frogs (*Hyla cinerea*) could only detect the presence of conspecific calls when the broadband background noise was spatially separated from the source of the call, but were unable to detect conspecific calls when they were in direct proximity to the broadband noise (Schwartz and Gerhardt, 1989). Barrass also found that traffic noise disrupted mating cues and altered reproduction of both the American green tree frog and Woodhouse's toad (Barrass, 1985). Specifically, it was found that the frequency, inter-call-interval and call duration of male calls varied significantly near highway noise. More importantly, female mate selection was significantly affected by the presence of traffic noise. For example, *B. woodhousei* females from sites frequently exposed to high traffic noise were fastest to respond to higher frequency male calls. On the other hand, females from a site with no previous exposure to traffic noise were fastest to respond to normal frequency *B. woodhousei* calls. This pattern was also found in *H. cinerea* females from low traffic exposure sites. They reacted faster to normal frequency calls than females from high exposure and moderate exposure sites. However, females from sites with high traffic exposure reacted faster than females from low and moderate sites when the call rate and frequency was increased (Barrass, 1985). The exposure to traffic noise may have important evolutionary consequences for this species as the results of this study indicate that high levels of traffic noise alter female mate choice. The females found in sites seldom exposed to traffic noise more easily detected lower frequency frog calls, perhaps indicating a preference for lower frequency calls. In contrast females preferred high frequency calls as their exposure to traffic noise increased, this is likely because traffic noise is typically found in the lower frequency ranges (Barrass, 1985; Parris et al., 2009). Most importantly, Barrass demonstrated that the total egg mass for both *B. woodhousei* and *H. cinerea* was reduced when they were located in close proximity to highway noise; suggesting that traffic noise can also have important negative fitness effects on frog populations.

While it may seem beneficial for males to increase their call transmission over a noisy environment by modifying call components (e.g. frequency, amplitude, timing) these changes may also negatively affect their mating opportunities if these changes are in opposing directions of female mate preference. Throughout anuran species there is a substantial diversity of female mate preference, which is often very complex (Parris et al., 2009). Female preference can be influenced by the call frequency, rate (number of calls per minute), duration, amplitude, call length or pulse rate (Gerhardt and Klump, 1988; Howard and Palmer, 1995; Parris et al., 2009). Generally, female frogs prefer calls that have a high energetic cost for the males producing them (Parris et al., 2009). Costly calls could be an honest indicator of high quality genes in a male. This is explained by the "good genes" hypothesis, which states that females will receive indirect benefits if they choose males who have genes that allow them to be more successful in their environment (Hamilton and Zuk, 1982; Welch et al., 1998). For instance, in some species female frogs prefer low frequency calls to higher frequency vocalizations, because the ability to produce lower frequency calls is generally correlated with greater body size (Gerhardt, 1994). However, in environments with high anthropogenic noise pollution male frogs often shift to higher frequency vocalizations (Kaiser et al., 2011).

Color as a Mode of Communication

In most species a female's choice of mate is not solely dependent upon her perception of a single male characteristic. Multiple factors are usually taken into account. In frogs, vocalizations may make up one (albeit very large) component out of many that females select between when choosing a mate. However, female frogs are also commonly attuned to male coloration.

Maan and Cummings found that female strawberry poison frogs (*Oophaga pumilio*) use male dorsal coloration in their selection of mates (Maan and Cummings, 2008). Although the females paid little attention to spotting patterns, females from orange populations were found to discriminate against green males. It was also found that females pay more attention to color than other population specific traits like behavior or size of the males (Maan and Cummings, 2008). Thus the *O.pumilio* females do seem to exhibit choosiness. Interestingly in a close relative of *O.pumilio*, the granular poison frog (*Oophaga granulifera*), significant differences in call properties are found between red and green color morphs, suggesting that male coloration, along with vocalizations, plays a role in female mate choice (Brusa et al., 2013). Nocturnal European tree frogs (*Hyla arborea*) have been shown to prefer males with vocal sacs that are more intensely colored when the calls produced by the males are equally attractive. They also chose males with a more conspicuous flank stripe over other males with less visible stripes (Gomez et al., 2009). It has been found that male *M.olmonae* have visibly lighter arm coloration than the rest of their body, possibly suggesting that this coloration may be used for communication (Vanko, 2012).

Color production, however, can have its disadvantages. Coloration, like vocalizations and other display traits may be costly for the male to produce. There are often indirect costs such as less energy distribution to other traits, or direct costs such as increased likelihood of predation associated with display traits (Sullivan and Kwiatkowski, 2007).

Biology of the Bloody Bay Poison Frog (*Mannophryne olmonae*):

No data currently exists on the effects of anthropogenic noise pollution on the vocalizations of the Bloody Bay Poison Frog (*Mannophryne olmonae*) calls. *M. olmonae* is endemic to the island of Tobago in the southern Caribbean. They are also found on the IUCN red list, a list created by the International Union for Conservation of Nature that catalogues the conservation status and distribution of plants and animals to determine their risk of extinction, where they are currently classified as vulnerable. Although the cause of *M.olmonae*'s 80% population decline in 2001-2004 is still unknown, the populations are now believed to be stable (Novick, 2012). However, very little research has been done on this species. In this study I examined the effects of traffic noise on ten aspects of *M. olmonae* calls: pulse duration, pulse rate, inter-pulse interval, low frequency, high frequency, change in frequency, dominant frequency, high amplitude, low amplitude, and upper harmonics. I also provide preliminary data on the function of arm color in female mate choice. This study has the potential to shed light on the effect of human-driven environmental change on this species, therefore contributing to our knowledge about the threats faced by the Bloody Bay Poison Frogs.

METHODS

Study Site

All research was conducted on the island of Tobago in the southern Caribbean. Thirty-five sites around the eastern end of the island were chosen as recording sites. These sites were already part of a long-term *M. olmonae* monitoring study, and therefore were prime survey sites (McQuigg, 2013; Novick, 2012) (Figure 1).

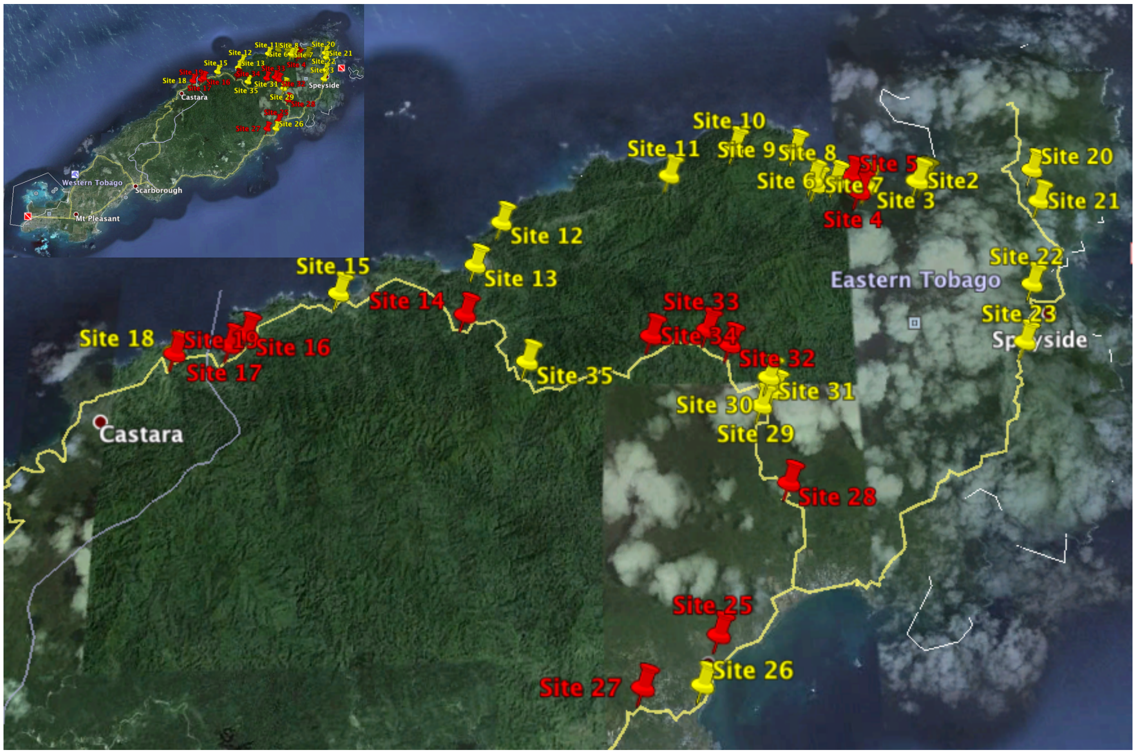

Figure 1. A map of Eastern Tobago inset with a map of the whole island, showing the location of each recording site (obtained from Google earth). Each red pin designates a recording site at which no *M. olmonae* calls were recorded for any survey of that site and each yellow pin designates a recording site at which *M.olmonae* calls were recorded during at least one visit to that site. The pale yellow lines represent roads.

Call Surveys

The call recordings of this diurnal species were collected between some of *M.olmonae's* peak calling hours of 15:00-18:00 (Alemu et al., 2007; R.M Lehtinen personal communication, November 18, 2013). Their peak hours occur between 8:00-9:30 and 15:00-18:00, which likely correspond to the hours during which the most traffic is on the roads (R.M Lehtinen personal communication, November 18, 2013). Each site was visited 2-3 times between the dates of June 4- June 8 2013. These dates fall during Tobago's rainy season, during which the height of *M. olmonae* reproduction occurs (R.M Lehtinen personal communication, November 18, 2013). During each site visit, a 2-minute recording was made and the humidity, temperature, GPS location as well as the level of anthropogenic disturbance were all noted. A Tascam DR-40 Linear PCM Digital Recorder and a Sennheiser ME66 Short Shotgun microphone with a wind baffle were used to record *M. olmonae* calls. All calls were recorded as 16-bit .wav files with a sampling rate of 44.1 kHz. Weather variables were measured using a Kestrel-4000 (manufactured by Nelsen-Kellerman Co.). The level of anthropogenic disturbance was determined using a C-weighted sound level meter from Radio Shack (catalogue number: 33-2055). The highest sound level reading observed during the 2-minute recording period was recorded as the anthropogenic noise disturbance level (dB) for that site visit. This reading is simply a snapshot of the sites' acoustic environment, however I am confident this is a representative measurement because the observed traffic levels did not vary a great deal between each visit. Nonetheless, in order to obtain a more representative snapshot, the total level of anthropogenic disturbance for each site was established by taking the average of all sound level readings during each site visit. Sites with high levels of anthropogenic disturbance were determined to be those with sound level readings of 68dB and above, while low disturbance level sites were those with anthropogenic noise not exceeding 67dB. This cutoff was chosen because there was a natural break in the average sound level (dB) data range at 67 dB (Figure 2). Also, similar cutoff ranges between high and low sites have been used in other studies on the effect of traffic noise on frog calls (Barrass, 1985; Cunnington and Fahrig, 2010). In addition to *M.olmonae* call comparisons at high and low traffic sites, I compared all ten aspects of the calls between sites containing waterfalls and sites without waterfalls. This was done in order to compare the potential masking response of *M.olmonae* between different low-frequency masking sources.

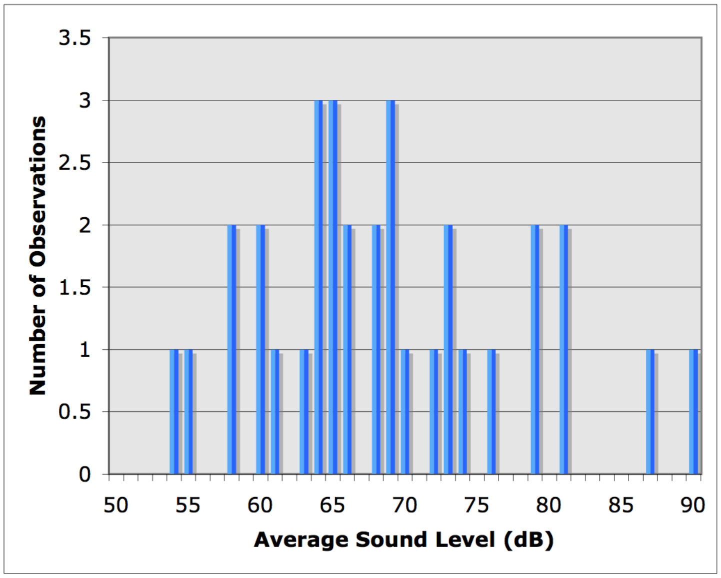

Figure 2. A histogram detailing the occurrence of average sound levels for all 34 sites.

Sonogram Analysis

The clearest recording from each site was analyzed using Raven Pro (version 1.4, Cornell Lab of Ornithology). Ten variables for each call and/or pulse were measured: Pulse Duration (s), Pulse Rate (s), Inter Pulse Interval (s), Low Frequency (Hz), High Frequency (Hz), Change in Frequency (Hz), Dominant Frequency (the frequency at which the maximum power (dB) occurred), High Amplitude and Low Amplitude (Figure 3). I also assessed the presence of Upper Harmonics, which are shown in Figure 4.

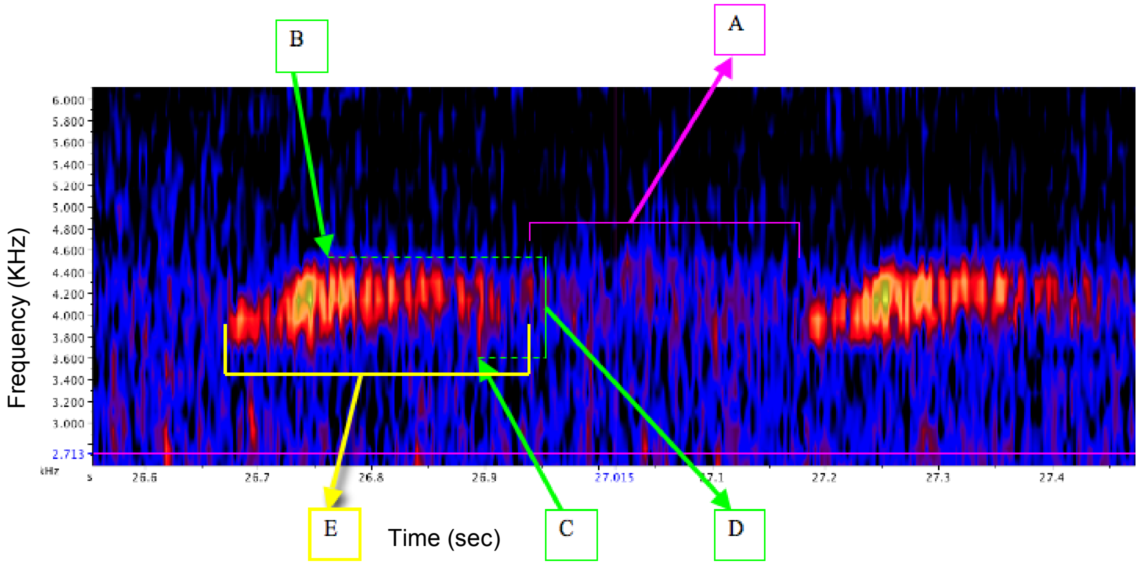

Figure 3. A sonogram of a *M. olmonae* call. A= inter-pulse interval, B= maximum frequency, C= minimum frequency, D= change in frequency, E= pulse duration. The amplitude is indicated by the shade of color (green/yellow= high, red/purple= low).

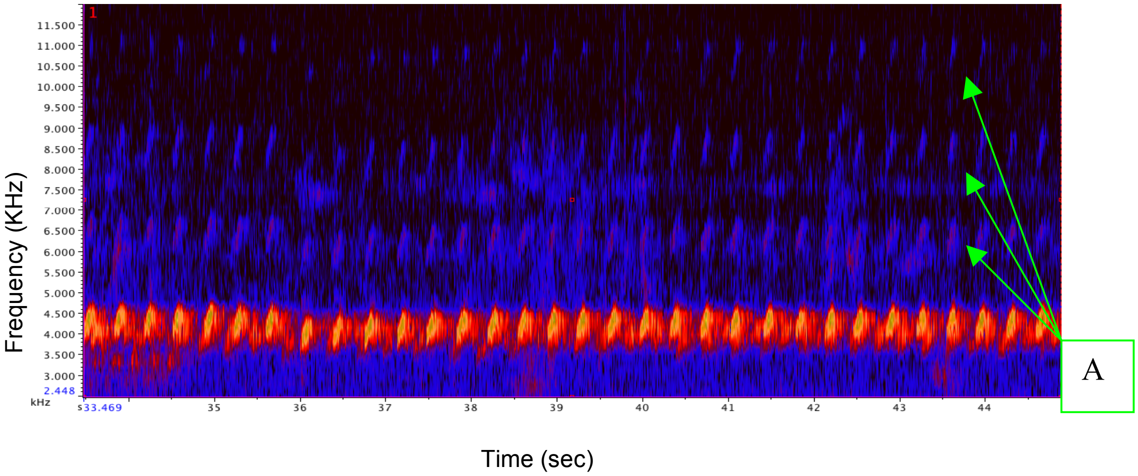

Figure 4. A sonogram of a *M. olmonae* call with upper harmonics (A= upper harmonics)

Statistical Analysis

The occurrence of upper harmonics was analyzed using Fisher's exact test. Pearson Correlations were run to test for the relationship between each variable of the male *M. olmonae* calls (with transformations if needed) and air temperature. Temperature correction is often necessary when studying frog vocalizations because it has been shown to have significant effects on call frequency (R.M Lehtinen personal communication, November 18, 2013). However, in this study no significant relationships were detected between temperature and any of the call characteristics, so no temperature correction was performed. Independent Samples T-tests were run separately for all ten variables with high/low anthropogenic noise disturbance (dB) as the distinguishing variable. This high/low method was chosen over other approaches (such as a linear regression) because this data contains only one independent variable and multiple dependent variables. Due to the exploratory nature of this study I made no corrections for multiple comparisons (Whitlock and Schluter, 2009). The goal of this study was to explore possible patterns in the data. This will allow future researchers to further examine the findings of my study. All statistical analysis was performed in SPSS version 21.0.

Color Pilot Study

Female *M. olmonae* Collection

Seven female *M. olmonae* were collected by hand from a stream running through a site west of the village of Castara. Each female was kept in a plastic container with leaves and water from their home stream for no more than one night before testing.

Set Up

A T-maze (0.816 m x 0.486 m x 0.349 m) was set up in an indoor laboratory with markings along the edges every 3 cm in order to measure the female's movement within the container (Figure 5). Two Cambridge SoundWorks (model #GCS300) speakers were placed directly opposite each other just outside either end of the maze (32.13 in apart) in front of a fabric covered opening. The call stimulus was broadcast at 78 dB - the amplification of a typical *M. olmonae* male call at a 1m distance in the wild - from a computer using Raven Pro (version 1.4, Cornell Lab of Ornithology) (Lehtinen et al., 2011). One dummy (either treatment or control) was placed in front of each speaker in a random pattern (Figure 5A). The dummies were small store bought toys approximately the same size and shape as *M.olmonae* males. The control dummy was painted only black, while the treatment was painted black with orange arms (Figure 5B). The treatment and control frogs were randomly placed at the beginning of each trial.

During the acclimation period, one female was placed under an acoustically transparent cone at the end of the T-Maze while a male call was played through both speakers for 3 minutes. After acclimation, the cone was lifted and the 3-minute trial began. During the trial the male call continued playing from each speaker and the female's movements, location, and direction were tracked. Every time a female moved, the direction of her movement (left/right, to back of t-maze, towards/ away from end of t-maze where control/treatment male is located etc.), as well as the distance of her movement were both recorded. A few other behaviors were noted. Whenever a female displayed an "alert" position- when the female straightens her two front arms while elevating her head and body- the direction she was facing was noted. A "head turn" and the direction of the turn was noted whenever a female's body remained stationary but her head rotated. "Escape behavior" was noted whenever a female jumped onto the side of the container and climbed toward the top of the container. A positive reaction was recorded when a female came within 10 cm of a male dummy and was oriented toward the dummy.

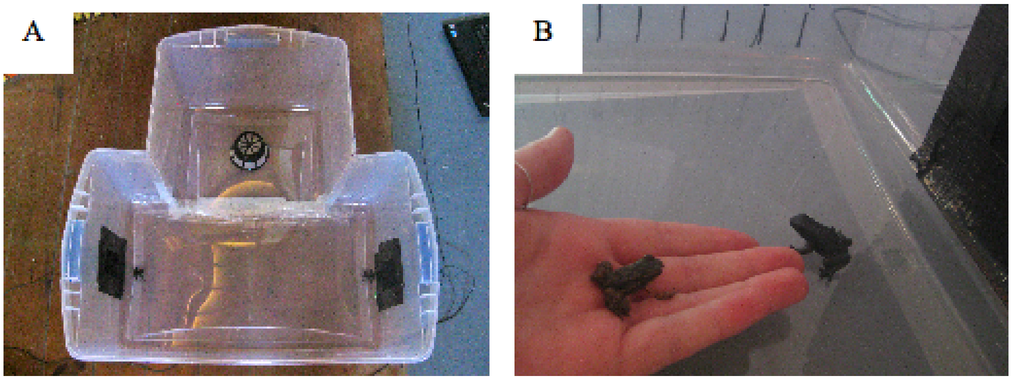

Figure 5. (A) The experimental set up for the female color preference study. The orange male dummy is on the right, while the black male dummy is on the left. (B) A female *M. olmonae* (in hand) and a male *M .olmonae* dummy.

RESULTS

The data from the color pilot study were not analyzed, as I could not collect enough females for a sample of sufficient size. However, statistically significant differences were detected in *M.olmonae* vocalizations between sites with low and high anthropogenic noise in three acoustic variables: high frequency, change in frequency and inter-pulse interval. Significantly higher frequencies, as well as a significantly larger difference between a call's low and high frequencies were found in areas of high anthropogenic noise. There were also significantly longer pauses between the end of one pulse and the beginning of the next pulse in areas of high anthropogenic noise. This is shown in Table 1 as well as Figures 6,7 and 8, respectively. There was also a significant difference found in the mean change in frequency between sites containing a waterfall and sites without a waterfall (p= 0.025) as shown in Figure 9. No significant differences were found between high and low anthropogenic noise sites in the pulse rate, pulse duration, low frequency, dominant frequency, the presence of upper harmonics, high amplitude, or low amplitude. However, there were two strong trends found between high and low anthropogenic traffic noise sites in both pulse duration, and the presence of upper harmonics. There was a strong pattern towards a longer duration of pulses in areas of low traffic noise compared to areas of high traffic noise (p=0.066). The amount of upper harmonics increased in sites with low anthropogenic traffic noise (p=0.080).

Variable	p-value	t-value	Low Mean (SD)	High Mean (SD)
Pulse Rate (pulses per sec)	0.116	1.649	3.891 (1.266)	3.04 (1.099)
Pulse Duration (sec)	0.066	1.952	0.178 (0.062)	0.135 (0.0362)
Low Frequency (kHz)	0.237	1.222	3.460 (185.102)	3.271 (453.439)
High Frequency (kHz)	0.014	-2.697	4.632 (199.219)	4.960 (333.955)
Change in Frequency (kHz)	0.027	-2.483	1.172 (245.885)	1.689 (639.584)
Dominant Frequency (kHz)	0.638	-0.479	4.112 (159.758)	4.148 (183.415)
ln Inter-Pulse Interval (sec)	0.025	-2.426	-2.944 (0.827)	-2.002 (0.943)
ln High Amplitude (dB)	0.97	0.038	5.432 (0.309)	5.425 (0.519)
ln Low Amplitude Squared (dB)	0.855	-0.185	10.813 (0.682)	10.884 (0.989)

Table 1. Results of nine acoustic variables measured in the male *M. olmonae* advertisement calls at sites with low anthropogenic noise and high anthropogenic noise on the island of Tobago.

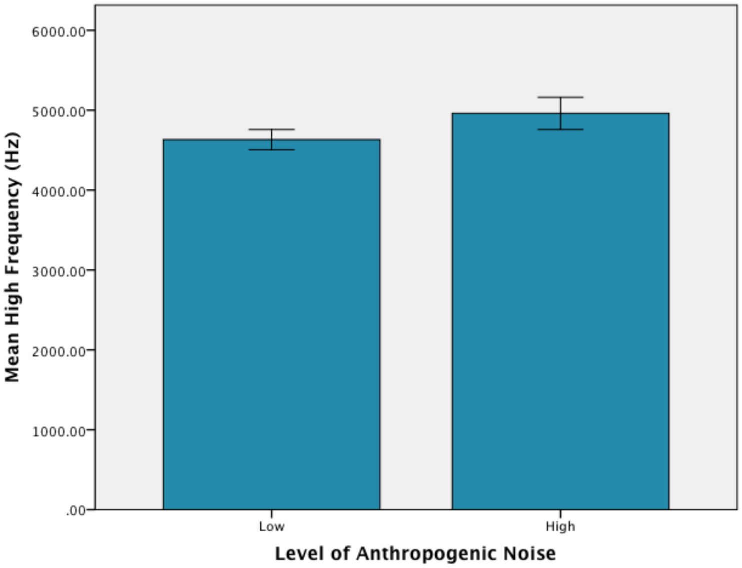

Figure 6. The mean highest frequency (Hz) of male *M.olmonae* calls recorded in sites on the island of Tobago with low levels of anthropogenic traffic noise and high levels of anthropogenic traffic noise. Significantly higher frequencies were found in areas of high traffic noise compared to those areas with low traffic noise (p=0.014). Error Bars: +/- 2 SE.

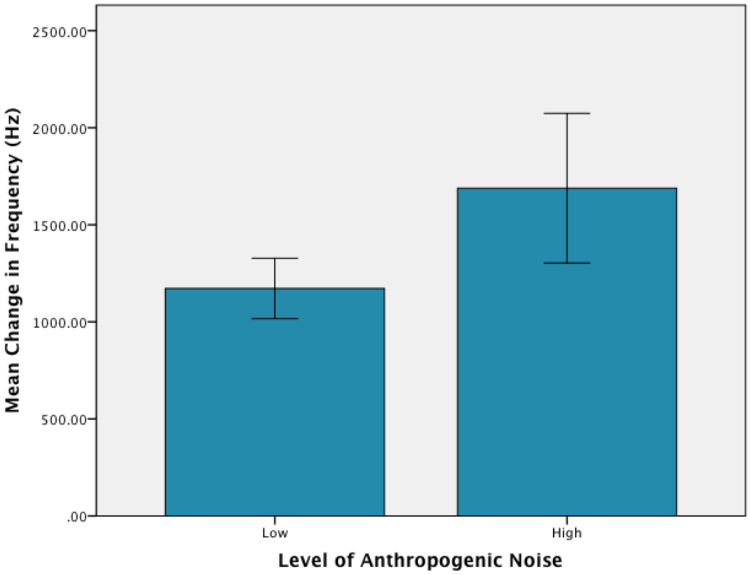

Figure 7. The change in frequency (Hz) of male *M.olmonae* calls recorded in sites on the island of Tobago with low and high levels of anthropogenic noise. A significantly greater difference between the high and low frequencies in *M.olmonae* calls was found in areas of high anthropogenic noise compared to areas with low levels of traffic noise (p=0.027). Error Bars: +/- 2 SE

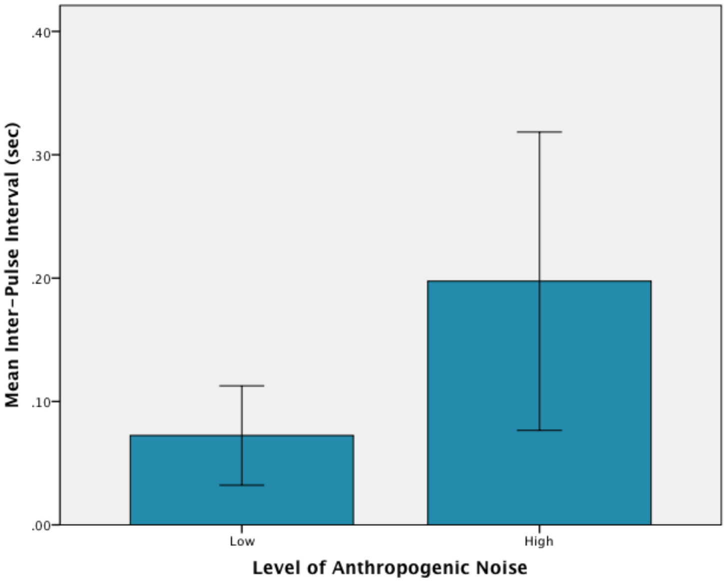

Figure 8. The mean inter-pulse interval (sec) of male *M.olmonae* calls in sites with high and low levels of anthropogenic noise and sites with high levels of anthropogenic traffic noise on the island of Tobago. Significantly longer pauses between the end of a pulse and the beginning of the next pulse were found in areas of high levels traffic noise compared to areas with low levels of traffic noise (p=0.025). Error Bars: +/- 2 SE.

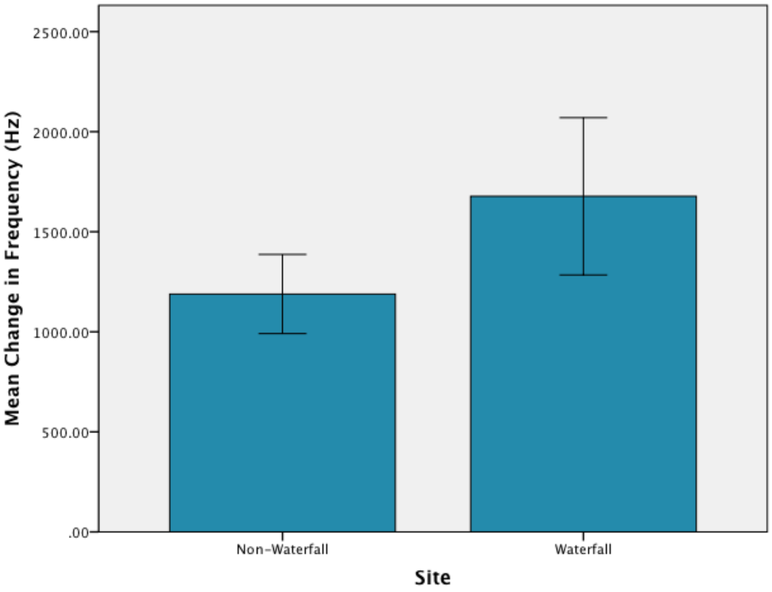

Figure 9. The mean change in frequency (Hz) of male *M.olmonae* calls in waterfall and non-waterfall sites on the island of Tobago. A significant increase in *M.olmonae* calling frequency was found in sites containing waterfalls compared to sites without waterfalls (p= 0.025). Error Bars: +/- 2 SE.

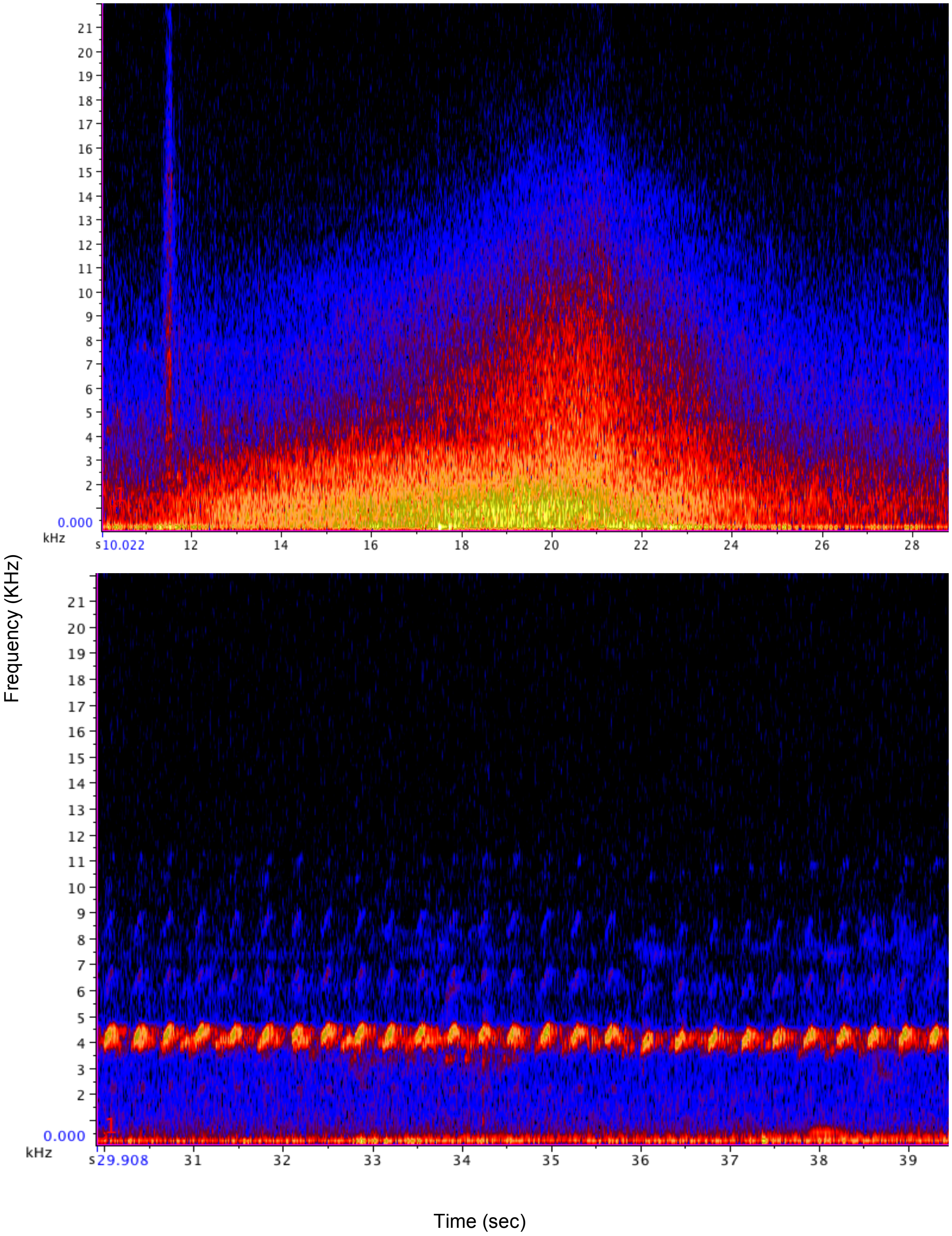

Figure 10. Spectrograms of male *M.olmonae* advertisement calls. The top spectrogram shows the dramatic increase in amplitude and broad low-frequency masking due to noise from a passing car. The bottom spectrogram shows an *M.olmonae* call in an undisturbed environment. In contrast to the top spectrogram, the upper harmonics and the pulses are both easily visible.

DISCUSSION

Outcomes for the Bloody Bay Poison Frog

This study's findings suggest that noise created by passing automobile traffic has significant effects on *M.olmonae* vocalizations. Specifically, this noise pollution leads to an increase in the upper frequency ranges of calls and an expansion of the total frequency range in which the calls occur. It is also important to note that no significant difference was found in low frequencies of frog calls between sites with high levels of anthropogenic noise (high noise sites) and those with low levels of anthropogenic noise (low noise sites). The fact that the frogs in high noise sites were only increasing their upper frequencies, and weren't expanding into the lower frequency ranges, suggests that there is a need for higher frequencies in areas of high anthropogenic traffic noise. These findings indicate that such vocal modifications are likely an attempt to escape from the low-frequency masking of traffic noise.

Waterfalls and other sources of fast-flowing water have also been proposed to mask the calls of other anurans (Grafe et al., 2012; Preininger et al., 2009; Tuttle and Ryan, 1982). My comparison between *M.olmonae* calls at waterfall sites and non-waterfall sites also supports my masking avoidance hypothesis. *M.olmonae* living in habitats containing waterfalls showed a significant upward increase in their change in frequency and a non-significant but noteworthy trend of increasing frequencies. These corresponding frequency trends in areas of both high traffic noise and waterfall noise suggest that these frequency alterations are used to reduce low-frequency masking from various sources.

A similar but not identical sensitivity to traffic noise has been found in previous studies conducted on other anuran species. In order to escape from low-frequency masking, other species have shifted to higher dominant frequencies in the presence of anthropogenic noise (Barrass, 1985; Cunnington and Fahrig, 2010; Parris et al., 2009). My study found no significant shift in dominant frequency, meaning that they didn't shift the frequency to which they deliver the most energy. This indicates that *M. olmonae* either is not able to or does not need to shift its dominant frequency. Often morphological constraints on body size make it impossible to shift vocalizations to higher or lower dominant frequencies even if it would be advantageous (Gerhardt, 1994; Grafe et al., 2012). Alternatively, the increase in high frequencies may be a way to balance species-specific interactions (that favor low frequency calls) with the increased traffic noise (that lowers the range over which the low-frequency calls can carry). In other words, natural selection may be in conflict with our inadvertent artificial selection.

A similar conflict, the conflict between sexual selection and natural selection has been widely studied in many species. The most famous example of this is in peacocks. Large extravagant peacock tails are highly beneficial for males when it comes to attracting female mates. However, they can be cumbersome when foraging for food or trying to hide and escape from predators (Smith, 1991). In a similar way, natural selection (including sexual selection) may be at odds with the artificial selection imposed on frogs by anthropogenic traffic noise. Female frogs of some species show a preference for low-frequency male calls, as they imply higher fitness in males. In these species males who are larger in size tend to have lower frequency calls (Murphy and Gerhardt, 2000; Ryan, 1983). Males who increase the dominant frequency of their calls, may reduce their reproductive opportunities and/or may mate with less fit females (Kaiser and Hammers, 2009; Parris et al., 2009). However, shifting to higher frequency ranges does not simply alter male-female interactions, it can have many consequences for male-male encounters as well (Arak, 1983; Cocroft and Ryan, 1995; Davies and Halliday, 1978; Kaiser and Hammers, 2009; Wagner, 1989).

Males compete with each other for territory and mates. Thus, a higher frequency shift indicates lower fitness to other males, alters the antagonistic interactions between males, and may even lead to reduced territory sizes (Kaiser and Hammers, 2009; Parris et al., 2009). Male frogs have been found to attack smaller males and retreat from conflict when confronted by larger males. This decision to fight or flee is made by a frequency analysis of the other male’s call (Arak, 1983; Davies and Halliday, 1978; Wagner, 1989). It is important to note, however, that this cannot be assumed to be true for *M.olmonae*. The mating system of *M.olmonae* has not yet been studied and may not be conventional. *M.olmonae* does show reverse sexual dimorphism and a study on a close relative of *M.olmonae*, *Mannophryne trinitatis*, found that females (not males) of that species were territorial (Wells, 1980).

One way to increase the frequency of the call without altering the frequency of the original waveform is to include upper harmonics. The vocalizations of various anuran species, including *M.olmonae*, contain upper harmonics (Chen et al., 2011; Lardner and

Lakim, 2004; Murphy and Gerhardt, 2000; Ryan and Rand, 2003). In the *M.olmonae* calls analyzed in this study, there was a clear (but non-significant) trend of increasing the frequency of upper harmonics in low noise sites compared to high noise sites (p= 0.08). This trend seems counterintuitive, upper harmonics would appear to be beneficial when lower frequencies of the frog's call are masked by traffic noise. Upper harmonics could serve to increase the frequency of the call, allowing it be heard above the noise pollution. However, it could be that the upper harmonics of *M.olmonae*'s call provide only negligible benefits. Therefore, this reduction in upper harmonics could be an energy saving technique. More studies must be performed in this area in order to determine what benefits (if any) *M.olmonae*'s upper harmonics provide. It would be helpful to perform playback studies with both lower and higher frequencies of anthropogenic traffic noise. This could determine whether or not the frogs are able to alter the amount of upper harmonics in their calls plastically depending on the frequency of the noise pollution.

Some frogs have the ability to alter aspects of their calls within their lifetime, this plasticity is shown in green frog (*Rana clamitans*), northern leopard frog (*Rana pipiens*), gray treefrog (*Hyla versicolor*) and other species of frogs (Bee et al., 2000; Cunnington and Fahrig, 2010; Reichert, 2010; Schwartz and Wells, 1983). However, some species of frogs do not demonstrate vocal plasticity and may not have the ability to react plastically to a changing environment (Cunnington and Fahrig, 2010; Kaiser and Hammers, 2009; Lengagne, 2008). These species can only alter their call parameters through evolution by natural selection.

So, how are *M.olmonae* changing the frequency and inter-pulse intervals of their vocalizations? At the present the answer remains unclear. They may have adapted over generations to an increasingly noisy environment. However, the most parsimonious explanation is vocal plasticity. Future research needs to be done in order to determine the answer. One study that would be helpful in this area is to find out if the populations in low traffic sites and high traffic sites are able to interbreed. If populations from two sites that differ in their noise components can breed, then the gene flow between the two populations would create intermediate offspring, making the evolution of different calls due to natural selection unlikely. It would also be beneficial to perform playback studies in areas of low traffic. Playback studies would allow us to see if the frogs do adjust their calls immediately in response to noise, which would indicate the ability for vocal plasticity.

This study also found significantly different inter-pulse intervals, and a non-significant but clear trend in pulse duration between low and high noise sites. Longer intervals between the end of each pulse and the beginning of the next were found in sites with high noise levels. The pulse duration in low noise sites was much longer than in high noise sites. When taken together, these two findings make sense: increasing inter-pulse intervals and decreasing call rate should go hand in hand. These paired results suggest that there is a real correlation between high levels of traffic noise and calls with both shorter pulses and longer pauses between each pulse that cannot be attributed to sampling or measuring error.

Similar results have been found in *Microhyla butleri*, *Rana nigrovittata* and *Kaloula pulchra*; all three species decreased their call rate in response to motorcycle and airplane flyover noise (Sun and Narins, 2005). Decreased call rate ("bout duration") in response to traffic noise was also found in the European tree frog (*Hyla arborea*) (Lengagne, 2008). A study on Emilio's ground frog (*Eupsophus emiliopugini*) found that the length of the call rate was dependent on the amplitude of the interfering noise: the call rate was higher at lower amplitudes of synthetic call noise and lower at higher amplitudes of synthetic noise (Penna and Hamilton-West, 2007). It is possible that such alterations could be an energy saving strategy. Calling is one of the most energetically costly behaviors a frog will ever undertake (Grafe, 1997; Wells and Taigen, 1989). In fact, a frog's aerobic metabolism may increase up to 22 times its normal resting rate while it is calling (Bucher et al., 1982; Prestwich et al., 1989; Wells and Taigen, 1989). Calls with a shorter duration presumably involve less non-aerobic costs than lengthier calls (Welch et al., 1998). In a study on male *Hyla microcephala*, the energetic cost of calling was found to increase as the number of notes in the call increased (Wells and Taigen, 1989). Thus it seems reasonable to assume a reduction in pulse rate and an increase in inter-pulse intervals may be energy saving techniques, as a frog would be using less energy each time it calls. However, there have been conflicting results from similar studies. This may be partially due to the fact that I could only find a handful of studies that clearly defined the meaning of each term they use to describe aspects of the calls. For example: 'note', 'pulse', 'call' and 'bout' are used to refer to the same characteristic of a frog call in some studies, while in other studies they are completely different terms. This means that distinguishing inter-pulse intervals from inter-call intervals can be virtually impossible if no clear definition is given in the study. As a result of this wide variation of unstandardized terminology, cross-species call comparisons are very difficult.

Be that as it may, I did come upon several studies with clearly defined but differing results to mine. A study on *B. woodhousei* toads found that they escaped the masking of anthropogenic traffic noise by increasing their call rate and lengthening the duration of their calls. It was also found that the pulse rate (called “pulse repetition rate” in the original study) was highly variable between the study sites. In the same study, *H. cinerea* was shown to escape masking through increasing their inter-call intervals and dominant frequency (Barrass, 1985). A study on the effects of motorcycle noise and music on the call rate of the Amazonian treefrog (*Dendropsophus triangulum*) found that male *D.triangulum* increased their call rates in response to both stimuli (Kaiser and Hammers, 2009). An increase in the call rate of *Rana taipehensis* was also found in response to airplane flyover and motorcycle noise (Sun and Narins, 2005).

This pattern of increasing call rates has not only been found in studies on the effects of anthropogenic noise. A study on *Hyla microcephala* males that were studied in the context of a chorus setting reduced their call rate as the number of other males in the chorus decreased, and when the amount of frogs calling in the chorus grew they increased their call rate (Wells and Taigen, 1989). Similar results have been elicited from studies on the effects of natural water, wind, rain and chorus noise on frog calls (Penna et al., 2005).

Calling at higher amplitudes is a common strategy that many animals use to lessen the masking effects of anthropogenic noise. Many mammalian, avian and some anuran species are able to change the amplitude of their vocalizations in reaction to increased background noise (Brumm and Slabbekoorn, 2005; Lengagne, 2008). However, the frogs in my study didn’t show any significant change in the amplitude of their calls. The most likely explanation for this is the extreme energy cost needed to increase amplitude. In order to achieve the same masking release as a 123 Hz increase in frequency, a frog would have to use up 37% more energy every night just to increase the amplitude of its call by 1.4dB (Parris, 2002; Parris et al., 2009).

One final strategy for masking reduction is the possible evolution of multimodal communication. Many anuran species near noisy water sources have evolved a behavior known as foot-flagging, during which a male frog will extend his hind leg(s) behind him and slowly stretch it back in an arc-like movement before returning it to his side (Hodl and Amezquita, 2001). For instance, the Bornean rock frog (*Staurois parvus*), which lives in environments with continuous low-frequency broadband noise due to fast running water, has been found to display several visual communication techniques (including foot flagging) along with it acoustic advertisement call (Grafe et al., 2012). The Brazilian Torrent frog (*Hylodes asper*) has, as its name suggests, evolved near torrents. The males of this species, along with concentrating the energy of their calls in the third harmonic, use foot-flagging to attract the attention of females (Haddad and Giaretta, 1999). The Panamanian golden frog (*Atelopus zeteki*), which lives along mountainous streams, relies preferentially on visual displays such as forefoot waving (Lindquist and Hetherington, 1996). In the dart-poison frogs (*Epipedobates femoralis*), a close relative of *M.olmonae*, vocal sac vibration and other visual cues were found to be required for aggression to be elicited in male-male interactions (Narins et al., 2003).

Impacts on Evolution, Ecology and Conservation

The evolution of multimodal communication has evolved in other species of frogs living near noisy water sources. Such an adaptation would likely benefit *M.olmonae* and other species whose calls are masked by traffic noise. However, the development of multimodal communication and call alteration may foreshadow more alarming changes that could arise if masking due to anthropogenic noise continues. Females of several species prefer lower frequency calls that indicate higher levels of male fitness (Kaiser and Hammers, 2009). This could lead to a tradeoff between audibility and attractiveness in male anurans. In turn, this could result in lower breeding success and even population extinction in otherwise suitable habitats (Kaiser and Hammers, 2009). These possible impacts should be investigated in *M.olmonae*. It would be beneficial to study how female preference is affected by male call alterations due to the interference of anthropogenic noise. This could be done in a similar fashion to my female preference study of male arm coloration; two identical dummies could be placed in front of speakers that alternately play either an unaltered call (from an area of low traffic noise) or the same call that has been manually altered to have increased frequency, longer inter-pulse intervals and shorter pulse durations. Fitness consequences should also be examined with long-term studies that investigate the relationship between *M.olmonae's* calling levels and reproductive success.

In general road traffic imposes periods of synthetic noise on natural environments, restricting those environments previously accustomed to relative quietude, to short intervals of silence interrupted by intermittent and unpredictable bouts of high amplitude and low frequency noise. The construction of roads, and infrastructure expansion slices up land into smaller and smaller slivers of undisturbed areas. Habitat fragmentation is a large issue for these species of frogs, and although it is rarely considered, the acoustic landscape can be fragmented just like physical habitats (Lynch et al., 2011).

Frogs and toads are often considered to be indicator species, warning us of the consequences of human caused environmental degradation before other species show the effects (Andreone and Luiselli, 2000; Barinaga, 1990). Studies like this one, which demonstrate the effects of anthropogenic noise on frog behavior, call attention to the importance of recognizing the impacts of our modifications to the environmental soundscape. These studies bring conservation into a new light; we don't simply need to conserve habitats, we need to conserve the acoustics of the habitats as well. Birds and frogs have already shown significant alterations in their call properties in the presence of anthropogenic noise (Bee and Swanson, 2007; Brumm, 2006; Dowling et al., 2012; Francis et al., 2009; Kaiser and Hammers, 2009; Lengagne, 2008; Parris, 2013; Parris et al., 2009; Slabbekoorn and Peet, 2003; Slabbekoorn and Ripmeester, 2008). My study focuses solely on the affects of noise on vocal communication, however, many other sounds are just as important as direct communication for the survival of many animals.

For example, the California ground squirrel (*Spermophilus beecheyi*) compares the rattles of the Pacific rattlesnake (*Crotalus viriaus oreganos*), in order to determine the danger it may pose to their pups (Swaisgood et al., 2003). Believe it or not, eavesdropping is as common in nature as it is in the human world, and it can mean the difference between life and death. Many animals rely on sound to determine the proximity and identity of other animals, whether they are predators, prey, competitors or potential mates (Lynch et al., 2011). Superb fairy-wrens (*Malurus cyaneus*) have learned to eavesdrop on predator alarm calls of noisy miners (*Manorina melanocephala*) in habitats where the two species coexist (Magrath and Bennett, 2012). Termites eavesdrop too. The drywood termite (*Cryptotermes secundus*) uses vibro-acoustic cues to distinguish between its more dangerous competitor, the subterranean termite (*Coptotermes acinaciformis*), and other members of its own species (Evans et al., 2009).

A great deal of information about human impacts on soundscapes remains unexplored, as we have only recently become aware of our acoustic impacts. The door is wide open for research on the effects of anthropogenic noise on the communication of frogs, birds, insects and all other sound-sensitive organisms. This research becomes more and more necessary as the exponential growth of the human race continues. The ever-growing human population demands more resources every generation. With each new person, we need more: more houses, oil, gas, meat, vegetables, fruit, water, land...and the list goes on. The heart of the issue is that we need more space. However, as we encroach on other species' habitats, it is important to remember that we don't just alter the landscape - we alter the soundscape. Understanding our impacts on the acoustic environment is imperative if we want to retain a diversity of acoustically communicating species. In the end, we must find a way to create harmony between our needs and the needs of all other species that occupy this earth.

ACKNOWLEDGEMENTS

I would like to thank my Senior Independent Study adviser Dr. Richard Lehtinen for his guidance and patience; this study would have been impossible without his support, advice and vast knowledge of anuran species. I would also like to thank my Junior Independent Study adviser Dr. Liliana D'Alba for her assistance in fleshing out my ideas into a full I.S. proposal, and my second reader Dr. Seth Kelly. I also want to thank Dr. Laura Sirot for her years of advice and for her animal behavior class, which prompted me to come up with this idea for my Independent Study project. A big thank you to Sara Green, Zak Bradley and John Murphy for all their help and moral support on the ground in Tobago. I want to thank my parents, Laura and Bill Clemmens, for their unwavering support through the entire I.S. process and my college career. I also want to thank my grandmother Barbara Ingraham for her encouragement and helpful edits. Asanteni sana to my friends, without whom I probably would have finished this study months earlier (but wouldn't have had half as much fun). Finally, I would like to thank my funding sources: the Copeland Fund and the College of Wooster Biology Department.

LITERATURE CITED

Alemu, J.B., Cazabon, M.N.E., Dempewolf, L., Hailey, A., Lehtinen, R.M., Mannette, R.P., Naranjit, K.T., and Roach, A.C.J. (2007). Ecological observations on the Critically Endangered Tobago endemic frog *Mannophryne olmonae*. Appl. Herpetol. *4*, 377–386.

Andreone, F., and Luiselli, L. (2000). The Italian batrachofauna and its conservation status: a statistical assessment. Biol. Conserv. *96*, 197–208.

Arak, A. (1983). Sexual selection by male–male competition in natterjack toad choruses. Nature *306*, 261–262.

Barinaga, M. (1990). Where Have All the Froggies Gone? Science *247*, 1033–1034.

Barrass, A.N. (1985). The Effects of Highway Traffic Noise on the Phonotactic and Associated Reproductive Behavior of Selected Anurans. Vanderbilt University.

Bee, M.A., and Swanson, E.M. (2007). Auditory masking of anuran advertisement calls by road traffic noise. Anim. Behav. *74*, 1765–1776.

Bee, M.A., Perrill, S.A., and Owen, P.C. (2000). Male green frogs lower the pitch of acoustic signals in defense of territories: a possible dishonest signal of size? Behav. Ecol. *11*, 169–177.

Boykoff, M.T., and Boykoff, J.M. (2004). Balance as bias: global warming and the US prestige press. Glob. Environ. Change *14*, 125–136.

Brumm, H. (2006). Animal communication: City birds have changed their tune. Curr. Biol. *16*, R1003–R1004.

Brumm, H., and Slabbekoorn, H. (2005). Acoustic Communication in Noise. In Advances in the Study of Behavior, C.T.S. Peter J. B. Slater, ed. (Academic Press), pp. 151–209.

Brumm, H., and Todt, D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. Anim. Behav. *63*, 891–897.

Brusa, O., Bellati, A., Meuche, I., Mundy, N.I., Pr&ouml, hl, H., and Rocha, L. (2013). Divergent evolution in the polymorphic granular poison-dart frog, *Oophaga granulifera*: genetics, coloration, advertisement calls and morphology. J. Biogeogr. *40*, 394–408.

Bucher, T.L., Ryan, M.J., and Bartholomew, G.A. (1982). Oxygen Consumption during Resting, Calling, and Nest Building in the Frog *Physalaemus pustulosus.* Physiol. Zool. *55*, 10–22.

Chen, Q., Cui, J., Fang, G., Brauth, S.E., and Tang, Y. (2011). Acoustic Analysis of the Advertisement Calls of the Music Frog, *Babina daunchina*. J. Herpetol. *45*, 406–416.

Cocroft, R.B., and Ryan, M.J. (1995). Patterns of advertisement call evolution in toads and chorus frogs. Anim. Behav. *49*, 283–303.

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B., and Peterson, R.O. (2002). Actividad de Vehículos para Nieve y Respuestas de Stress Glucocorticoide en Lobos y Alces. Conserv. Biol. *16*, 809–814.

Cunnington, G.M., and Fahrig, L. (2010). Plasticity in the vocalizations of anurans in response to traffic noise. Acta Oecologica *36*, 463–470.

Davies, N.B., and Halliday, T.R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. Nature *274*, 683–685.

Dowling, J.L., Luther, D.A., and Marra, P.P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. Behav. Ecol. *23*, 201–209.

Evans, T.A., Inta, R., Lai, J.C.S., Prueger, S., Foo, N.W., Fu, E.W., and Lenz, M. (2009). Termites Eavesdrop to Avoid Competitors. Proc. Biol. Sci. *276*, 4035–4041.

Everest, F.A., Pohlmann, Ken C (2009). Master handbook of acoustics (New York: McGraw-Hill).

Forman, R.T.T., and Alexander, L.E. (1998). Roads and their major ecological effects. Annu. Rev. Ecol. Syst. *29*, 207–+.

Forrest, T.G. (1994). From Sender to Receiver: Propagation and Environmental Effects on Acoustic Signals. Am. Zool. *34*, 644–654.

Francis, C.D., Ortega, C.P., and Cruz, A. (2009). Noise Pollution Changes Avian Communities and Species Interactions. Curr. Biol. *19*, 1415–1419.

Gerhardt, H.C. (1994). The Evolution of Vocalization in Frogs and Toads. Annu. Rev. Ecol. Syst. *25*, 293–324.

Gerhardt, H., and Klump, G. (1988). Masking of Acoustic-Signals by the Chorus Background-Noise in the Green Tree Frog - a Limitation on Mate Choice. Anim. Behav. *36*, 1247–1249.

Given, M.F. (1999). Frequency Alteration of the Advertisement Call in the Carpenter Frog, *Rana virgatipes*. Herpetologica *55*, 304–317.

Gomez, D., Richardson, C., Lengagne, T., Plenet, S., Joly, P., Léna, J.-P., and Théry, M. (2009). The role of nocturnal vision in mate choice: females prefer conspicuous males in the European tree frog (*Hyla arborea*). Proc. R. Soc. B Biol. Sci. *276*, 2351–2358.

Grafe, T.U. (1997). Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. Anim. Behav. *53*, 1103–1117.

Grafe, T.U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J.M., Proksch, S., and Hoedl, W. (2012). Multimodal Communication in a Noisy Environment: A Case Study of the Bornean Rock Frog *Staurois parvus*. Plos One *7*.

Haddad, C.F.B., and Giaretta, A.A. (1999). Visual and Acoustic Communication in the Brazilian Torrent Frog, *Hylodes asper* (Anura: Leptodactylidae). Herpetologica *55*, 324–333.

Hamilton, W., and Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? Science *218*, 384–387.

Hartmann, W.M. (2013). Principles of musical acoustics. ([S.l.]: Springer).

Hodl, W., and Amezquita, A. (2001). Visual signaling in anuran amphibians. In Ryan MJ, ed. Anuran Commun. *Washington, DC: Smithsonian Institution Press.*, 121–141.

Howard, R., and Palmer, J. (1995). Female Choice in *Bufo-americanus* - Effects of Dominant Frequency and Call Order. Copeia 212–217.

Intergovernmental Panel on Climate Change (2007). Climate Change 2007: Impacts, Adaptation and Vulnerability.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., and von Toschanowitz, K.T. (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Model. *185*, 329–348.

Kaiser, K., and Hammers, J.L. (2009). The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, *Dendropsophus triangulum*. Behaviour *146*, 1053–1069.

Kaiser, K., Scofield, D.G., Alloush, M., Jones, R.M., Marczak, S., Martineau, K., Oliva, M.A., and Narins, P.M. (2011). When sounds collide: the effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America. Behaviour *148*, 215–232.

Keller, I., and Largiader, C.R. (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proc. R. Soc. B-Biol. Sci. *270*, 417–423.

Lardner, B., and Lakim, M. b (2004). Female call preferences in tree-hole frogs: why are there so many unattractive males? Anim. Behav. *68*, 265–272.

Lehtinen, R.M., Wojtowicz, E.A., and Hailey, A. (2011). Male vocalizations, female discrimination and molecular phylogeny: multiple perspectives on the taxonomic status of a critically endangered Caribbean frog. J. Zool. *283*, 117–125.

Lengagne, T. (2008). Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. Biol. Conserv. *141*, 2023–2031.

Lindquist, E.D., and Hetherington, T.E. (1996). Field Studies on Visual and Acoustic Signaling in the “Earless” Panamanian Golden Frog, *Atelopus zeteki.* J. Herpetol. *30*, 347–354.

Lopez, P., Narins, P., Lewis, E., and Moore, S. (1988). Acoustically Induced Call Modification in the White-Lipped Frog, *Leptodactylus-albilabris*. Anim. Behav. *36*, 1295–1308.

Lynch, E., Joyce, D., and Fristrup, K. (2011). An assessment of noise audibility and sound levels in U.S. National Parks. Landsc. Ecol. *26*, 1297–1309.

Maan, M.E., and Cummings, M.E. (2008). Female preferences for aposematic signal components in a polymorphic poison frog. Evolution *62*, 2334–2345.

Magrath, R.D., and Bennett, T.H. (2012). A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proc. Biol. Sci. *279*, 902–909.

McQuigg, J. (2013). A Reassessment of the Conservation Status of a Critically Endangered Neotropical Frog, *Mannophryne olmonae*, Using Occupancy Modeling Techniques. Sr. Indep. Study Theses.

Murphy, C.G., and Gerhardt, H.C. (2000). Mating Preference Functions of Individual Female Barking Treefrogs, *Hyla gratiosa*, for Two Properties of Male Advertisement Calls. Evolution *54*, 660–669.

Narins, P.M., Hödl, W., and Grabul, D.S. (2003). Bimodal signal requisite for agonistic behavior in a dart-poison frog, *Epipedobates femoralis*. Proc. Natl. Acad. Sci. *100*, 577–580.

Narins, P.M., Feng, A.S., and Fay, R.R. (2006). Hearing and Sound Communication in Amphibians (Springer).

Novick, A. (2012). Using Occupancy Modeling Techniques to Reevaluate the Conservation Status of the Critically Endangered Caribbean Frog, *Mannophryne olmonae*. Sr. Indep. Study Theses.

Parker, B.R. (2009). Good vibrations: the physics of music (Baltimore: Johns Hopkins University Press).

Parris, K. (2013). Anthropogenic noise constrains acoustic communication in urban-dwelling frogs. Proc. Meet. Acoust. *19*, 010055.

Parris, K.M. (2002). More bang for your buck: the effect of caller position, habitat and chorus noise on the efficiency of calling in the spring peeper. Ecol. Model. *156*, 213 – 224.

Parris, K.M., Velik-Lord, M., and North, J.M.A. (2009). Frogs Call at a Higher Pitch in Traffic Noise. Ecol. Soc. *14*.

Parsons, E.C.M., Dolman, S.J., Wright, A.J., Rose, N.A., and Burns, W.C.G. (2008). Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? Mar. Pollut. Bull. *56*, 1248–1257.

Patenaude, N.J., Richardson, W.J., Smultea, M.A., Koski, W.R., Miller, G.W., Würsig, B., and GReene, C.R. (2002). Aircraft Sound and Disturbance to Bowhead and Beluga Whales During Spring Migration in the Alaskan Beaufort Sea. Mar. Mammal Sci. *18*, 309–335.

Patricelli, G.L., and Blickley, J.L. (2006). Avian Communication in Urban Noise: Causes and Consequences of Vocal Adjustment. The Auk *123*, 639–649.

Penna, M., and Hamilton-West, C. (2007). Susceptibility of evoked vocal responses to noise exposure in a frog of the temperate austral forest. Anim. Behav. *74*, 45–56.

Penna, M., Pottstock, H., and Velasquez, N. (2005). Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest. Anim. Behav. *70*, 639–651.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., and Pieretti, N. (2011). Soundscape Ecology: The Science of Sound in the Landscape. BioScience *61*, 203–216.

Preininger, D., Boeckle, M., and Hödl, W. (2009). Communication in Noisy Environments Ii: Visual Signaling Behavior of Male Foot-flagging Frogs *Staurois latopalmatus*. Herpetologica *65*, 166–173.

Prestwich, K.N., Brugger, K.E., and Topping, M. (1989). Energy and Communication in Three Species of Hylid Frogs: Power Input, Power Output and Efficiency. J. Exp. Biol. *144*, 53–80.

Reichert, M.S. (2010). Aggressive Thresholds in *Dendropsophus ebraccatus*: Habituation and Sensitization to Different Call Types. Behav. Ecol. Sociobiol. *64*, 529–539.

Ryan, M.J. (1983). Sexual Selection and Communication in a Neotropical Frog, *Physalaemus pustulosus*. Evolution *37*, 261–272.

Ryan, M.J., and Rand, A.S. (2003). Sexual selection in female perceptual space: How female tungara frogs perceive and respond to complex population variation in acoustic mating signals. Evolution *57*, 2608–2618.

Schaub, A., Ostwald, J., and Siemers, B.M. (2008). Foraging bats avoid noise. J. Exp. Biol. *211*, 3174–3180.

Schwartz, J.J. (1993). Male Calling Behavior, Female Discrimination and Acoustic Interference in the Neotropical Treefrog *Hyla microcephala* under Realistic Acoustic Conditions. Behav. Ecol. Sociobiol. *32*, 401–414.

Schwartz, J., and Gerhardt, H. (1989). Spatially Mediated Release from Auditory Masking in an Anuran Amphibian. J. Comp. Physiol. -Sens. Neural Behav. Physiol. *166*, 37–41.

Schwartz, J.J., and Wells, K.D. (1983). The Influence of Background Noise on the Behavior of a Neotropical Treefrog, *Hyla ebraccata.* Herpetologica *39*, 121–129.

Slabbekoorn, H., and Peet, M. (2003). Ecology: Birds sing at a higher pitch in urban noise. Nature *424*, 267–267.

Slabbekoorn, H., and Ripmeester, E. a. P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. Mol. Ecol. *17*, 72–83.

Smith, J.M. (1991). Theories of sexual selection. Trends Ecol. Evol. *6*, 146–151.

Stearns, S.C., and Hoekstra, R.F. (2005). Evolution: an introduction (Oxford [England]; New York: Oxford University Press).

Sullivan, B.K. (1985). Male Calling Behavior in Response to Playback of Conspecific Advertisement Calls in Two Bufonids. J. Herpetol. *19*, 78–83.

Sullivan, B.K., and Kwiatkowski, M.A. (2007). Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. Funct. Ecol. *21*, 666–675.

Sun, J.W.C., and Narins, P.A. (2005). Anthropogenic sounds differentially affect amphibian call rate. Biol. Conserv. *121*, 419–427.

Swaisgood, R.R., Rowe, M.P., and Owings, D.H. (2003). Antipredator Responses of California Ground Squirrels to Rattlesnakes and Rattling Sounds: The Roles of Sex, Reproductive Parity, and Offspring Age in Assessment and Decision-Making Rules. Behav. Ecol. Sociobiol. *55*, 22–31.

Tuttle, M.D., and Ryan, M.J. (1982). The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. Behav. Ecol. Sociobiol. *11*, 125–131.

Vanko, A. (2012). Case of Natural Selection? the Effects of Invasive Bamboo and Local Geology on the Cryptic Coloration of the Bloody Bay Poison Frog. Sr. Indep. Study Theses.

Wagner, W. (1989). Graded Aggressive Signals in Blanchard Cricket Frog - Vocal Responses to Opponent Proximity and Size. Anim. Behav. *38*, 1025–1038.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. Nature *416*, 389–395.

Warren, P.S., Katti, M., Ermann, M., and Brazel, A. (2006). Urban bioacoustics: it's not just noise. Anim. Behav. *71*, 491–502.

Welch, A.M., Semlitsch, R.D., and Gerhardt, H.C. (1998). Call Duration as an Indicator of Genetic Quality in Male Gray Tree Frogs. Science *280*, 1928–1930.

Wells, K.D. (1980). Social Behavior and Communication of a Dendrobatid Frog (*Colostethus trinitatis*). Herpetologica *36*, 189–199.

Wells, K.D., and Taigen, T.L. (1989). Calling energetics of a neotropical treefrog, *Hyla microcephala*. Behav. Ecol. Sociobiol. *25*, 13–22.

Whitlock, M., and Schluter, D. (2009). The analysis of biological data (Greenwood Village, Colo.: Roberts and Co. Publishers).

Windle, R.J., Wood, S., Shanks, N., Perks, P., Conde, G.L., daCosta, A.P.C., Ingram, C.D., and Lightman, S.L. (1997). Endocrine and behavioural responses to noise stress: Comparison of virgin and lactating female rats during non-disrupted maternal activity. J. Neuroendocrinol. *9*, 407–414.

Wollerman, L. (1999). Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. Anim. Behav. *57*, 529–536.

Wood, W.E., Yezerinac, S.M., and Dufty, J. (2006). Song Sparrow (*Melospiza melodia*) Song Varies with Urban Noise. The Auk *123*, 650–659.