

IT TAKES TWO: THE SIMULATION OF A SOCIAL INTERACTION TO QUANTIFY
VARIATIONS IN ACOUSTIC CUES WITH ANIMAL POSITION AND HEAD
MORPHOLOGY

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TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	ii
TABLE OF CONTENTS.....	iv
LIST OF FIGURES.....	v
LIST OF TABLES.....	vi
CHAPTER 1. INTRODUCTION.....	7
Study Aims.....	13
Hypotheses.....	14
CHAPTER 2. METHOD.....	16
Animal Subjects.....	16
Procedure and Data Acquisition.....	17
Data Preparation and Analysis.....	19
Statistical Analysis.....	20
CHAPTER 3. RESULTS.....	22
Position and Power Spectral Density.....	22
Position and Harmonics.....	22
Placement and Power Spectral Density.....	23
Placement and Harmonics.....	23
The Interaction of Position and Placement.....	23
CHAPTER 4. DISCUSSION.....	27
Limitations.....	29
Future Research.....	30
FIGURES.....	31
TABLES.....	39
REFERENCES.....	40

LIST OF FIGURES

Figure 1. The experimental set up.....	31
Figure 2. a) DTAG placed on lower left jaw fat. b) DTAG placed on gular area. c) DTAG placed on lower right jaw fat.....	32
Figure 3. Adobe Audition spectrogram view of 4 sine type whistles from 1 hoop trial prior to each whistle being selected out for individual analysis.....	33
Figure 4. A MATLAB spectrogram view of 1 sine type whistle.....	33
Figure 5. Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by receiver position as recorded on DTAGs.....	34
Figure 6. Estimated Number of Harmonics, ± 1 SE, by receiver position as recorded on DTAGs.....	34
Figure 7. Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement as recorded on DTAGs.....	35
Figure 8. Estimated Mean Number of Harmonics ± 1 SE, by DTAG Placement as recorded on DTAGs.....	35
Figure 9. Estimated Mean Number of Harmonics ± 1 SE, by Interaction of DTAG Placement and Receiver Position as recorded on DTAGs.....	36
Figure 10. Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement in the 45° Receiver Position as recorded on DTAGs.....	37
Figure 11. Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement in the 90° Receiver Position as recorded on DTAGs.....	37
Figure 12. Estimated Mean Number of Harmonics, ± 1 SE by Position, as measured by the 4032 reference hydrophone, placed above the receiving animal.....	38

LIST OF TABLES

TABLE 1. <i>Summary statistics & general characteristics of whistles (N = 134) as measured by DTAG</i>	39
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Chapter 1. INTRODUCTION

An animal perceives its environment through sensory organs and then acts on that environment through its reactions and impulses, in order to understand the cognitive world of that animal it is important to try and understand that relationship (Delfour, 2010). Odontocetes (toothed whales) are incredibly well adapted to their marine environment and the driving sensory modality for these animals is hearing. The odontocete auditory sensory system is exceptionally well-developed and, of those species tested, displays the broadest range of frequency sensitivity in the animal kingdom (Branstetter & Mercado, 2006; Ketten, 2000). While the nature of an odontocete's perceptual experiences cannot be directly observed, it can be inferred by studying the animal's physiological capabilities, behavior, and environment (Delfour, 2010; Jerison, 1986; Mercado & DeLong, 2010; von Uexkull, 1982, 1992). By studying the hearing sensitivity of odontocetes, scientists gain insight into which auditory sensations in the environment these animals can perceive and in turn, which sounds may be most relevant. Furthermore, the ability to examine how odontocetes hear different frequencies dependent on where the sound is received on the body and from which direction it originates has significantly contributed to the understanding of how odontocetes might perceive their environment (Branstetter & Mercado, 2006; Pacini, 2011; Taylor, 2013). While it may be impossible to completely understand the cognitive world of an odontocete, additional insight will arise from the analysis of the sensory information available in their environment, and how their own bodies may affect the processing of that information (Kremers, 2013). The current research investigated some of the sensory information available to an odontocete in order to better understand the cognitive world of odontocetes.

Most mammals integrate cues within received sounds, such as time of arrival, intensity, and frequency, to interpret and identify their surrounding environment (Mooney, 2008a). Hearing sensitivity to directional cues and localization of sound sources are crucial characteristics of auditory sensory systems across taxa, as they enable an animal to identify positions of prey, predators, and conspecifics (Mooney et al., 2008b). Many species of the family Delphinidae (delphinids) are highly social, live in relatively large groups, and frequently use sound to communicate in both agonistic and affiliative contexts. These social odontocetes, such as false killer whales (FKW) (*Pseudorca crassidens*) and bottlenose dolphins (*Tursiops truncatus*), may use sounds from conspecifics to maintain coordination of movement during travel, while foraging, and for defense from predators while in a visually restricted environment or over large distances (Tyack & Clark, 2000). Odontocete vocalizations are hypothesized to contain salient cues that facilitate social cohesion in these and other contexts (Branstetter, Moore, Finneran, Tormey, & Aihara, 2011; Lammers, Au, & Herzing, 2003; Miller, 2002). For communication to be effective however, listeners must extract information from received phonations in order to represent their environment. Studies show that listeners across taxa, including birds, bats, elephants, primates, and hyenas are proficient in extracting information from both a signal and the context in which that signal is given (Seyfarth & Cheney, 2003). To understand and begin to interpret an odontocete's communication system and how an odontocete perceives communication signals, one must first determine what information is available in a communication signal and how changes in the environment could effect how that that signal might be processed.

Studies in both controlled and natural environments show that odontocetes are highly skilled in both actively and passively navigating their environment acoustically (Au, 1993;

Benoit-Bird & Au, 2009; Burros & Myrberg, 2005; Gannon et al., 2005; Xitco & Roitblat, 1996;). Xitco and Roitblat (1996) demonstrated that dolphins are even capable of “eavesdropping” (attending to, recognizing, and forming a mental representation of) on an object that another dolphin has ensonified. Renaud & Popper (1975) demonstrated that bottlenose dolphins are capable of acute localization of a sound source over a wide range of frequencies. Baird et al. (2010) found that several individually satellite-tagged FKW that were from a single group disassociated, occasionally moving more than 100 km apart, and re-associated over periods of days. In fact, these findings, from both controlled and natural environments, together imply the ability of FKW and bottlenose dolphin conspecifics to localize and coordinate their movements and direction of travel over great distances with no available visual aide, most likely through vocalizations between individuals. Bottlenose dolphin vocalizations were analyzed in a controlled environment in the current study in order to investigate specific cues within the signals that odontocetes might use in order to localize and coordinate their movements.

Odontocete vocalizations are usually classified into two broad functional categories, bio-sonar and communication. Echolocation clicks are known to function as a type of bio-sonar used for orientation, navigation, and foraging (Au, 1993), while whistles and burst-pulsed sounds are thought to function for communication with conspecifics (Herzing, 2000; Janik & Slater, 1998; Oswald et al., 2007). For the sake of relevance to the current study, whistles will be the only vocalization described hereafter. Whistles are continuous, narrow-band, tonal signals that are often frequency-modulated and have harmonic features. Analysis of whistles includes measures of classification such as contour, frequency modulation over time, duration, and peak frequency (Caldwell, Caldwell, & Tyack, 1990). Their duration can range from several tenths of a second to several seconds (Oswald, Rankin, Barlow, & Lammers, 2007; Tyack & Clark, 2000). A

whistle's frequency can span a range from 2 to 30 kHz and some whistles can have harmonic features with frequencies up to 100 kHz (Lammers et al., 2003; Oswald, Rankin, & Barlow, 2004). Many whistle characteristics are unique to a particular species. These properties allow for reliable species identification using solely acoustic measures for certain species. For example, bottlenose dolphin whistles have mean fundamental frequency ranges from 7.9-17 kHz and mean durations of 1 second, while FKWs have mean fundamental frequency ranges from 5.3-8.3 kHz and mean durations of 0.44 seconds. (Oswald et al., 2007; Rendell, Matthews, Gill, Gordon, & Macdonald, 1999). There is strong evidence that odontocetes are also capable of perceiving and discriminating these differing frequencies and frequency contours as well as auditory temporal differences (Ralston & Herman 1995; Thompson & Herman 1975; Yunker & Herman, 1974) For example, bottlenose dolphins can discriminate frequency differences of 0.3-0.4% and intensity differences as little as 1dB (Evans, 1973; Herman & Arbeit, 1972; Jacobs 1972). In fact, the FKW in the current study demonstrated the ability to discriminate complex, artificially generated, tones with varying harmonic content, which were similar to whistles (Yuen, Nachtigall, Breese, & Vlachos, 2007).

The aforementioned acoustic properties of whistles can be influenced by many factors, which the current study explores. Whistles have historically been described as being omnidirectional in nature due to their relatively low frequency content (Evans Sutherland, & Beil, 1964). However, there is evidence that whistles from several odontocete species do indeed have directional properties. Using a towed array in the wild, Lammers & Au (2003) found that the harmonic content of spinner dolphins' (*Stenella longirostris*) whistles change dependent on the location of a receiving hydrophone in reference to an individual signaling dolphin's orientation. This study corroborated Miller's (2002) finding from a similar experiment, that higher order

harmonics of killer whale calls were broadly directional. Both of these field studies provided indirect evidence for the directional properties of harmonic structures in whistles, which describe Larsen and Dabelsteen's (1990) "mixed directionality hypothesis" that low frequency elements (fundamental frequencies) of the whistle are more omnidirectional than higher frequency elements (harmonics) (Lammers & Au, 2003; Miller, 2002). However, orientation of signaling animals could not be precisely established in these field experiments, therefore more precise measurements were needed to confirm this hypothesis. Branstetter et al. (2011) provided further evidence of the mixed directionality of whistles by using a hydrophone array in laboratory measurements of outgoing whistles from a bottlenose dolphin. These three studies suggest that the spatial relationship between a whistling animal and a receiving animal can passively influence the harmonic characteristics of that whistle. These changes in the harmonic structures of a whistle at the receiver may function as localization and direction of movement cues to listening conspecifics.

The spatial relationship between signaling and receiving animals is only one factor to consider when deciphering the salient cues that are available to a signal-processing listener/receiver. According to the shaded receiver model of odontocete hearing, the head and the body of the receiving animal may also affect the intensity, as well as temporal and spectral components of a received whistle (Møhl, Au, Pawloski, & Nachtigall, 1999). Therefore characteristics of incoming whistles may also be channeled by the shape and composition of the receiver's head and body (Mooney et al., 2008b). Furthermore, in a behavioral study, Au & Moore (1984) found that sounds travelling to the inner ear of a receiving animal are differentially dependent on the position of the sound source relative to that animal. Hearing studies have

shown that there are areas of differing hearing sensitivities on the odontocete head (Møhl et al., 1999; Pacini, 2011; Popov, Supin, Ya, Klishin, & Bulgakova, 2003).

In sum, two decades of research have shown that: (a) odontocetes are capable of detecting and discriminating differing frequencies, contours, and harmonics in whistles (b) components of whistles are directional in nature (c) hearing sensitivities differ on different points of the head dependent on frequency, and (d) odontocetes may use all of these inputs to discern conspecific movement. However there are no studies precisely measuring odontocete whistles at various receiving angles and in different receiving positions around the head of the receiver. Despite the breadth of literature describing the directional hearing capabilities of some odontocetes as well as the notable but small number of studies demonstrating the directional properties of odontocete whistles, the sensory umwelt, or “subjective universe” (Delfour, 2010, p. 793), of odontocetes is still not entirely understood. There is still limited information describing the characteristics and changes of bioacoustic signals at an actual odontocete receiver. This information will contribute to our understanding of the interactive relationship between odontocetes and their subjective world. They might also help to explain and interpret observational field data indicating that odontocetes frequently travel together, disperse, and then reunite with ease.

Innovative methods and tools have been used and created in order to study the bioacoustics and communication systems of odontocetes in both controlled settings and in their natural environment. Digital archival tags (DTAGs) (Johnson & Tyack, 2003) have been used to study the acoustic behavior of cetaceans in their natural environment and provide an opportunity to record signals at an actual odontocete receiver. They can be attached to an individual's body via suction cups and record vocalizations made by the focal animal and by surrounding

conspecifics, as well as sounds in their environment. However, there are fundamental limits to interpreting the acoustic data that the tags provide. There are some difficulties in measuring the received sound produced by one animal and received by another. Because a tag is placed on the body of the animal acting as a sound source, the hydrophone receivers are inherently placed within the acoustic near-field of the focal animal sound source. A near-field measurement from a sound source does not allow for accurate measurements of an animal's source levels.

Furthermore, the focal animal's body, particularly its bones and air-filled structures, may shade and modify the acoustic path of an incoming conspecific's signal. Closely grouped conspecifics' bodies may also interfere with an incoming signal. Without visual representation of where other vocalizing animals are in reference to the recording tag, there is no way to know how accurately the recorded sound represents the original signal (Johnson, de Soto, Madsen, 2009; Oleson, et al. 2007; Zimmer, Johnson, Madsen, & Tyack, 2005a; Zimmer, Madsen, Teloni, Johnson, & Tyack, 2005b). It can also be difficult, especially among highly-social, closely-grouped, and fast-moving odontocetes, like FKWs and bottlenose dolphins, to accurately attribute recorded social calls and echolocation clicks to the tagged focal animal because of the aforementioned issues (Johnson et al., 2009). Currently reported data analyses from acoustic tags used in field studies do not account for body shading, and the distance and orientation of signaling individuals cannot always be established precisely. Therefore, received levels may be underestimated and directionality cues may be difficult to interpret.

Study Aims

The objective of this study was to measure the sounds available for one listening (receiving) animal to hear from the sounds that were produced by another signaling animal in order to determine if that receiver's spatial positioning and head shading affect the energy and

frequency content of an odontocete's communication signals. Controlled experiments were performed where the spatial relationship between two odontocetes (a signaler and a receiver) was measured at various angles. The independent variables (IV) in this study were the orientation of the receiver in reference to the signaler and the head of the "receiving" FKW. The dependent variable (DV) in this study was the acoustic content (the mean power spectral density of the fundamental frequency and mean number of harmonics) of the received signals. These experiments attempted to examine:

(1) the differences in the acoustic content of an odontocete whistle dependent on the orientation of a receiver relative to a signaler, and

(2) if and how the head of a FKW shades incoming odontocete communication signals.

A 4 element hydrophone system (a combination of a DTAG-3 along with two other individual hydrophones) was used to provide accurate measurements of changes in whistle characteristics dependent on both the spatial positioning of the signaler and receiver and on the shape of the receiver's head. The characteristics of recorded signals were compared across receiver spatial positions and DTAG placements. The purpose of the current research was to collect data that could reveal specific cues within an emitter's signal that may relay information to a receiver about the location and movement of a signaling animal and also to also provide precise measurements of acoustic parameters in a controlled environment and thus contribute to more accurate interpretations of acoustic behavior of individuals in their natural environment.

Hypotheses

For each main objective listed above, the following hypotheses have been established to answer two specific questions:

1. Does the head of a receiving odontocete shade an incoming whistle?

H0: Measurements of received levels and/or frequency content of an incoming odontocete's communication signal will not vary with head morphology of a receiving odontocete

H1: Measurements of received levels and/or frequency content of an incoming odontocete's communication signal will vary with head morphology of a receiving odontocete

2. Does the spatial orientation of a signaling odontocete relative to a receiving odontocete affect the characteristics of the signal at the receiver?

H0: The characteristics of a communication signal measured at a receiving odontocete will not vary with spatial positioning of a signaling odontocete relative to that receiving odontocete.

H1: The characteristics of a communication signal measured at a receiving odontocete will vary with spatial positioning of a signaling odontocete relative to that receiving odontocete.

Chapter 2. METHOD

The current study followed a protocol approved by the Institutional Animal Care and Use Committee of the University of Hawai'i at Mānoa (NMFS permit # 93.004.20).

Animal Subjects

Two odontocete subjects participated in the current study. Both animals resided in a floating pen complex at the Hawai'i Institute of Marine Biology's Marine Mammal Research Program (MMRP) located just off of Coconut Island in Kaneohe Bay, Oahu, Hawai'i. The adult female FKW, Kina, was under human care in Hawai'i since 1987. The exact age of this whale was unknown, however she was a sub-adult when she was brought to Hawai'i in 1987. At the time of this experiment this subject weighed 567.5 kg and measured 3.96 m. The adult female Atlantic bottlenose dolphin, BJ, was born in 1985 at the NOSC (Naval Ocean Systems Center) breeding colony at the Kaneohe Marine Corps Base. At the time of this experiment this subject weighed 189.6 kg and was 2.44 m long. Both animals had extensive experience with cooperative participation in a variety of echolocation and audiometric experiments (Kloepper, Nachtigall, & Breese, 2010; Kloepper, Nachtigall, Donahue, & Breese 2012; Nachtigall, Lemonds, Roitblat, 2000; 2008; Pacini, 2011; Yuen et al., 2007) and had participated in daily research and training sessions throughout their care at MMRP. At the time of this experiment Kina consumed approximately 14.54 kg of food per day and BJ consumed approximately 5.9 kg per day. Their diet was composed of a mixture of herring, capelin, and squid. Rewards during training and experimental sessions were based on a variable schedule of reinforcement. Any part of their rations that were not received as part of an experimental or training session were delivered throughout other parts of the day, regardless of the animals' performance during sessions. Kina

was trained in the receiver role and BJ in the role of signaler. Neither animal had been previously trained to perform whistles on cue or to participate in an experiment in tandem.

Procedure and Data Acquisition

The experiment and training sessions were conducted at MMRP. The test area was a 6x9 meter floating pen previously used in several other acoustic experiments (Yuen et al., 2007; Mooney, 2008a; Mooney et al., 2008b; Taylor, 2013), see Figure 1. The pen's netting allowed for sound to pass freely. The recording equipment and the researcher were set up in a test shack. There were two trainers involved in every session, one assigned to the listener (Kina) and one to the signaler (BJ).

The signaler's task was to enter a custom-made water-filled PVC hoop (that was fixed onto a beam that ran across the pen for support, see Figure 1. Once stationary, the signaler whistled on cue (SD= underwater light was controlled by trainer at the surface), and then returned to the trainer for reward. The receiver's task was to wear the DTAG-3, see Figure 2, and to enter a separate, custom-made water-filled PVC hoop (that was positioned at various angles and distances away from the signaler) and remain stationary, while the signaler completed several whistle trials, after which the listener was recalled to the trainer for reward, see Figure 1. The trained whistle behavior was initially captured by opportunistically rewarding a naturally produced whistle and then was subsequently paired with the SD. Both of the animals were initially trained individually for their respective tasks in the test pen and then trained in tandem.

Prior to the start of a trial, both the signaler and receiver stationed on separate vertically placed pads on the side of the pen near their respective trainers. When cued, the receiver swam into her hoop, with the guidance of her trainer's target pole, up to her pectoral flippers and remained stationary for the trial. After the receiver was in position the signaler was then cued to

swim into her hoop up to her pectoral flippers and remained stationary while she performed her whistle task. While in their hoops, both the signaling animal and the receiving animal stationed underwater at a depth of 1m, see Figure 1. The signaler's trainer was positioned on the deck in between an equipment shack and the pen. In order to confirm when the signaler whistled on cue, her trainer wore headphones that were connected to a hydrophone attached to the receiver's hoop via a splitter connected through the recording equipment.

The signaling animal's position was constant throughout each whistle trial in the experiment. The receiving animal was positioned at various angles and distances around the signaling animal while wearing a digital acoustic recording tag (DTAG-3), see Figure 2a. Measurements of angles and distances of the receiving animal in reference to the signaling animal were measured from the signaler's blowhole to the receiver's blowhole. The receiver's distance from the signaler was 2m at 45°, 90°, and 135°, and 6m distance at 180°, see Figure 1. For each receiver position there was three DTAG-3 placement locations on the receiver's head known to be involved in sound reception, the left jawbone, see Figure 2a, the right jawbone see Figure 2b, and the gular area, see Figure 2c. The receiving animal remained in the hoop for approximately 1 minute and 30 seconds at a time. The signaling animal entered and left the hoop for several whistle trials, for each of the respective DTAG-3 placements and receiving animal's angles, during the 1:30 trial.

Each session was video recorded both in-air and underwater, and all video recorded sessions were synched with all acoustic recordings. The experiment was video recorded in-air using a GoPro Hero 3 (GoPro, Inc., San Mateo, California) and a Canon Vixia HF20 (Canon, Tokyo, Japan) handheld video camera. Underwater video also recorded the signaler's hoop using an underwater camera (SCS Enterprises, Montebello, NY, USA). Timing was synched for all

recordings prior to running each session by a short acoustic signal. A human data recorder (using stopwatches that were synched with the acoustic recordings and videos) was assigned to visually observe each subject and to record each time the subject was positioned correctly in the hoop and when the subject moved out of position.

Acoustic recordings of each session were continuous for all hydrophones. Each condition's session was recorded underwater using two hydrophones, each occupying an independent channel: a Reson TC 4013 (Teledyne RESON, Slangerup, Denmark) with a receiving sensitivity of $-211 \pm 3\text{dB re } 1\text{V}/\mu\text{Pa}$ and an additional with 20 dB gain via a Khron Hite amplifier and filter (Khron Hite, Brockton, MA) and a Reson TC 4032 (Teledyne RESON, Slangerup, Denmark) with a receiving sensitivity of $-170\text{dB re } 1\text{V}/\mu\text{Pa}$ (with no gain). Both of these hydrophones were high pass filtered at 1 Hz (via the Khron Hite amplifier and filter). The signals were sent to a National Instruments DAQmx-PCI 6133 analog to digital board (A/D) board (National Instruments, Austin, TX), which digitized the signal at a sampling rate of 200 kHz. As illustrated in Figure 1, the Reson 4013 was always positioned 0° and 2m distance from the signaler's head (measured from blowhole) and at 1 m depth, and the Reson 4032 was attached to the listener's hoop pole, just above the listener's head at 1m depth. An archival digital recording tag, DTAG-3 (sampling rate 480 kHz, with a sensitivity of $-175\text{ dB re } 1\text{V}/\mu\text{Pa}$) was attached to the receiver's head in three separate placements: facing, the side of the lower jaw facing the signaler, gular, and away, the side of the lower jaw not facing the signaler (the hypothesized "shaded" side), see Figure 2.

Data Preparation & Analysis

Video data, hand written data, and the start of a short acoustic signal were all used to confirm the timing of each whistle trial in the audio file for each session. Whistles from each trial

were then manually extracted from each hydrophone recording using Adobe Audition 3.0, see Figure, 3. Because the signaler's whistles were not stereotyped, only whistles that were frequency modulated and had whistle contours that were shaped like a sine wave were selected for analysis, see Figure 3 & 4. The fundamental frequencies were analyzed for each whistle and the total number of visible harmonics for each whistle was counted. A total of 142 sine type whistles were recorded on all 3 hydrophones, of those 8 were thrown out due to interference from electrical noise in the recordings. A total of 134 sine type whistles were selected for analysis, see Table 1. Each whistle was analyzed using a custom written MATLAB analysis program. The signal to noise ratio (SNR), energy flux density (EFD), mean power spectral density (PSD), duration, and frequency ranges were calculated for each whistle. Of the 134 whistles selected for analysis, 95 whistles recorded on the DTAG had a SNR>0 (SNR<0: n=39); of the whistles recorded on the 4013, 110 had a SNR > 0 (SNR<0: n=24); and of the whistles recorded on the 4032 SNR>0 = 106 (SNR<0 n=28). There was significant natural background noise due to the snapping shrimp population in Kaneohe Bay. Snapping shrimp produce loud broad-band repetitive clicks that can not be completely filtered out of the signal due to the frequency modulated nature of the signaler's whistles, see Figure 4. Since EFD measurements sum the energy from the entire frequency band, EFD measurements intrinsically include noise as well as the targeted signal. The number of whistles with a SNR above 0 in this sample was relatively few within the separate positions and DTAG placements, therefore the average PSD (in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), which calculates the level of the peaks above the noise floor around the measured signal within a selected frequency band, was used as the a dependent variable measure in final analysis. The average PSD was calculated from 6 evenly spaced points along the whistle frequency contour, see Figure 4. This measurement allowed for inclusion of whistles regardless

of their SNR, as the peak energy above the noise in the selected frequency was measured at these points. The mean number of harmonics was measured within and across each receiver position as well as within each DTAG placement across those positions as a second dependent variable, see Figure 3 & 4.

Statistical Analysis

Preliminary measurements from the on-axis hydrophone (4013) recordings revealed that there was significant variability in the signaler's whistles' mean PSD across each position. Additionally, correlation analysis indicated that the mean PSD and that the number of harmonics per whistle were moderately correlated, $r=.53$, $p<.001$. Therefore, a multivariate analysis of covariance (MANCOVA) was conducted to determine whether the mean PSD and the number of harmonics varied as a function of DTAG placement (i.e. on the facing jaw, away jaw, or gular area) and receiver position (45°, 90°, 135°, and 180°), while controlling for whistle variability (Tabachnick & Fidell, 2007).

Chapter 3. RESULTS

The characteristics of the whistles analyzed from the DTAG in this study can be seen in Table 1. MANCOVA results using Wilks' criterion indicated that the combined dependent variables (the mean PSD and the number of harmonics) were significantly related to the covariate (the 4013 mean PSD= whistle variability), $F(2, 121) = 16.85$, $p < .001$, to position, $F(6, 242) = 10.62$, $p < .001$, to DTAG placement, $F(4, 242) = 10.24$, $p < .001$, and to the interaction between position and placement, $F(10, 242) = 3.74$, $p < .001$. Test of between-subjects effects indicated that all independent variables (DTAG placement, receiver position, 4013 PSD, and the interaction between position and placement) were significantly associated with change in both mean PSD and number of harmonics individually, with the exception of the position/placement interaction, which did not significantly predict change on mean PSD, $F(5, 133) = 1.06$, $p = .38$. Post hoc testing was therefore conducted to determine the nature of the mean PSD differences in position and placement separately.

Position & PSD

Post hoc testing using the Bonferroni correction indicated that the estimated mean PSD for the 45° position was significantly greater than all three other positions, the 90° position (mean difference = 8.42, $p < .001$), the 135° position (mean difference = 5.53, $p = .02$), and the 180° position (mean difference = 9.17, $p < .001$), see Figure 5. There were no other significant differences in mean PSD across other positions. A somewhat similar relationship emerged when the same post hoc testing was used to compare the number of harmonics across the 4 receiver positions.

Position & Harmonics

The estimated number of harmonics in the 45° position was significantly greater than that of two positions, the 90° position (mean difference = .81, $p < .001$) and the 180° position (mean difference = 1.04, $p < .001$). The number of harmonics in the 135° position was also greater than that of the 180° position (mean difference = .70, $p = .001$), see Figure 6. There were no other significant differences in the number of harmonics across other positions.

Placement & PSD

Post hoc testing using the Bonferroni correction indicated that the mean PSD also varied as a function of the DTAG placement on the receiver's head when examining PSD without considering position of the receiver. Estimated mean PSD in the facing placement group was significantly greater than mean PSD measured in the away placement group (mean difference = 3.00, $p = .04$) and the estimated mean PSD measured in the gular placement group was significantly greater than the mean PSD measured in the away placement group (mean difference = 4.93, $p = .001$), see Figure 7.

Placement & Harmonics

Post hoc testing using the Bonferroni correction indicated that the number of harmonics also varied as a function of the DTAG placement on the receiver's head when examining the number of harmonics without considering position of the receiver. The number of harmonics in the facing placement group was significantly greater than number of harmonics measured in the away placement group (mean difference = .87, $p < .001$) and in the gular placement group (mean difference = .51, $p = .01$), see Figure 8.

The Interaction of Position and Placement

As noted above, the number of harmonics, but not the DTAG PSD, varied significantly as a function of the interaction between the receiver position and the DTAG placement, see Figure

9. Therefore, post hoc testing was conducted to determine the estimated mean number of harmonics recorded in each individual position/placement combination. The estimated mean difference in the number of harmonics between the facing and away head placements decreased substantially as the position of the receiver moved from in front of the signaler to behind the the signaler. For example, the mean number of harmonics recorded by the facing DTAG was 2.00 (221%) greater than that of the away DTAG in the 45° position, while the mean number of harmonics recorded by the facing DTAG was only 0.14 (23%) greater than that of the away DTAG in the 180° position. However, these results revealed the unexpected finding that the estimated mean number of harmonics was lowest in the gular placement at the 90° position.

Because there was no significant interaction effect on DTAG mean PSD measured between position and placement, ANCOVAs were also performed separately to compare mean PSD at the three DTAG placements at each individual receiver position. Two interesting findings were revealed in these analyses. The greatest differences were found in the 45° and the 90° positions. In the 45° position, the estimated mean PSD measured on the facing DTAG placement was significantly higher than the away DTAG placement $F(2,31) = 5.36, p = .01$, even when accounting for whistle variability, see Figure 10. Furthermore, in the 90° position, the mean PSD was significantly higher in the gular DTAG placement than in the away DTAG placement $F(2,36) = 3.29, p = .05$, see Figure 11. Significant variance across DTAG head placement was not found in either the 135° or 180° positions.

To determine whether DTAG placement unduly influenced measurements of mean PSD and number of harmonics across receiver positions, whistles recorded only from the reference hydrophone (Reson 4032) were also analyzed, while controlling for whistle variability. Using Wilks' criterion, the combined dependent variables (the mean PSD and the number of

harmonics) were significantly related to the covariate (the 4013 mean PSD= whistle variability), $F(2, 121) = 20.00$, $p < .001$, to position, $F(6, 242) = 9.32$, $p < .001$, and to DTAG placement, $F(4, 242) = 3.06$, $p = .02$, but they were not related to the interaction between position and placement, $F(10, 242) = 1.37$, $p = .20$.

Post hoc testing using the Bonferroni correction indicated that on the 4032 reference hydrophone the estimated mean PSD for the 45° position was significantly greater than all 3 other positions: greater than the 90 degree position (mean difference = 6.11, $p < .001$), greater than the 135° position (mean difference = 6.90, $p < .001$), and also greater than the 180° position (mean difference = 6.96, $p < .001$). There were no other significant differences in mean PSD across the positions when measuring just from the 4032. Post hoc testing using the Bonferroni correction also indicated that on the reference hydrophone the estimated mean number of harmonics for the 45° position was significantly greater than all 3 other positions: greater than the 90 degree position (mean difference = 1.05, $p < .001$), greater than the 135° position (mean difference = 0.67, $p = .04$), and also greater than the 180° position (mean difference = .89, $p = .001$). While DTAG placement did not have an impact on the measurements of mean PSD, DTAG placement appeared to have some impact on the mean number of harmonics across the 4 receiver positions.

Similar post hoc testing also indicated a significant mean difference between the mean number of harmonics recorded by the 4032 when the DTAG was in the facing placement versus the away placement on the receiver's head (mean difference = .39, $p = .04$). To determine whether this affected the main analyses, an additional ANCOVA was performed to determine whether position and placement still affected the number of harmonics measured by the DTAG after controlling for the number of harmonics measured by the 4032 reference hydrophone and

whistle variability. Position, placement, and the interaction between position and placement all retained the same significant association with the number of harmonics recorded by the DTAG in this analysis, with modest increases in F values across all independent variables.

Chapter 4. DISCUSSION

The results presented in this study indicate that there is directionality in the whistle communication signals of a bottlenose dolphin, based on both the energy within the fundamental frequency and the harmonic structure of the signal. These results not only confirm previous research demonstrating that higher harmonic frequencies are directional (Branstetter et al., 2011; Lammers & Au, 2003; Miller, 2002); they also describe the independent directionality of the fundamental frequency alone. Measurements of both harmonic structure and energy at the fundamental frequency taken at 45° ahead of a signaling dolphin demonstrate the strongest confirmation of the tested hypotheses. In this experiment, at 45° ahead of the signaling dolphin, received fundamental frequencies of whistles were stronger in energy than those received at any position behind 45°. The directionality of the fundamental frequencies of the whistles analyzed in this study, as demonstrated by their decreasing strength behind the 45° position, is an interesting finding, as other whistle directionality research (Branstetter et al., 2011; Lammers & Au, 2003; Miller, 2002) describes fundamental frequencies of whistles as being more or less omnidirectional.

Whistles were also directional as measured by harmonic structure when they were recorded on the 4032 reference hydrophone, which was unaffected by head shading. The harmonic structure of these whistles was richest at 45° and degraded in positions behind 45°. The harmonic structure also varied when the whistles were measured from the DTAGs, however the DTAG placement did have an affect on these measurements, with the lowest mean harmonics measured in the 90°gular position. Given that a similar trend was found when examining whistles received by the 4032 reference hydrophone, it is likely that this finding is due to either whistle variability between individual experimental sessions or measurement error, and should

be interpreted with caution. Despite this unexpected finding, these measures indicate that the harmonic structure of a signal decreases when the receiver moves behind the signaler.

The results also suggest that head shading of received whistle communication signals does occur at a receiving FKW. This head shading is demonstrated by the variability in the measurements of the energy and the harmonic structure of whistles received on three sides of a receiving FKW's head. Whistles measured on the DTAG head placement that was facing the signaler had more energy in the fundamental frequencies and were richer in harmonic structure than whistles measured from the DTAG that was attached on the other side of the FKW's head. In these DTAG measurements in 45° position, harmonics decreased incrementally as placement moved from facing to gular to away. As mentioned above, however, this trend did not persist in the 90° position, where harmonics measured in the gular position were lower than in any of the other placements across all receiver positions. This anomalous finding limits the interpretability of these results. One possible way to interpret this is that harmonics vary as expected when the receiver is in front of the signaler, but because the signals are directional, they attenuate in unreliable ways once the receiver moves to the side and behind the signaler. This study also found that in the 45° position and the 90° position, there was some effect of head shading on fundamental frequency as well. As would be expected, in the 45° position the strongest signal was received on the DTAG placement facing the signaler and surprisingly (and contrary to the findings related to harmonics), in the 90° position the strongest signal was received on the gular DTAG placement.

Taken together, these findings suggest that, at least at close range, changes in call energy and harmonic structure due to signaler orientation relative to conspecific listeners may provide cues that relay information about the signaler's direction of movement or orientation. It is

currently unknown if dolphins intentionally transmit specific information in order to elicit a specific response from a conspecific, however it is known that dolphins use certain whistles in certain contexts (Janik & Slater, 1998). The current research demonstrates that when a listener is ahead of a signaler, the received signal contains more energy and is richer in harmonic structure than a signal received parallel to or behind that signaler. This suggests that a signaler could orient in a way to broadcast more directly to certain individuals or to groups of individuals. Furthermore, this research provides evidence that head shading changes energy and spectral characteristics of a signal from one side of the head to another, especially when a receiving animal is ahead of a signaling animal. These energy and spectral differences may be the cues that a receiver processes in order to localize the position and direction of travel of a signaling animal. The data provided from this research can be used to better interpret the findings of communication studies of wild animals that utilize attached acoustic recording tags to record communication signals of animals travelling in groups.

Limitations

The signal to noise ratio was a significant limitation in the analysis of the whistles in this study. The environmental noise that was captured in the recordings significantly limited the number of whistles that could be analyzed compared to previous studies in quieter environments. Therefore an adaption in the analysis method was developed for this study and a mean value of power spectral density was used instead of the energy flux density or the typical single power spectral density value. While this is a significant limitation, such an adaptation may be relatable to collecting data in the field where noise cannot be controlled and where snapping shrimp are prevalent in some areas. The fact that significant hypothesized findings emerged despite the limitations of this method suggests that mean power spectral may offer a promising method of

analyzing dolphin whistles that occur within the context of significant interference from snapping shrimp or other similar environmental noise.

Equipment limitations also influenced the quality of the data collected in this experiment. The lack of multiple hydrophones with equal sensitivity limited the ability to compare the number of harmonics across all recording hydrophones. The differing sensitivities of the hydrophones influenced the capability of the hydrophone to receive harmonics, which in turn made the visual representation of the harmonics on the spectrogram unreliable across the different recordings. The limited number of hydrophones prevented the same whistle from being analyzed and compared across all locations and placements. Therefore whistle measurements were aggregated for analysis and their mean values were compared across positions and placements, thus potentially limiting the interpretation of this data.

Future Research

While there is now substantial evidence that there are available cues within a whistle that a listening odontocete could sense and use to identify the location and direction of travel of a signaling conspecific, it is unknown if odontocetes actually perceive, attend to, and respond to these cues. More controlled studies are needed to better understand the way that sounds are perceived by animals distributed spatially around a signaler. Orientation of animals in field studies should also be observed to confirm that the 45° angle has some significance in transmitting cues for directionality of movement. Furthermore, simultaneously DTAGing multiple odontocetes in the field and correlating the signals and orientation changes of the tagged animals while using results from this and other controlled studies to better inform the interpretation of this field data may also be useful in advancing our understanding of odontocete communication.

FIGURES

Figure 1. The experimental set up in the pen: the signaling bottlenose dolphin (left) positioned in the hoop at 1 m depth and the 5 positions of the receiving false killer whale. The hydrophone on axis of the signaler is the Reson 4013 while the reference hydrophone, attached to the receiver's hoop pole, is the Reson 4032.

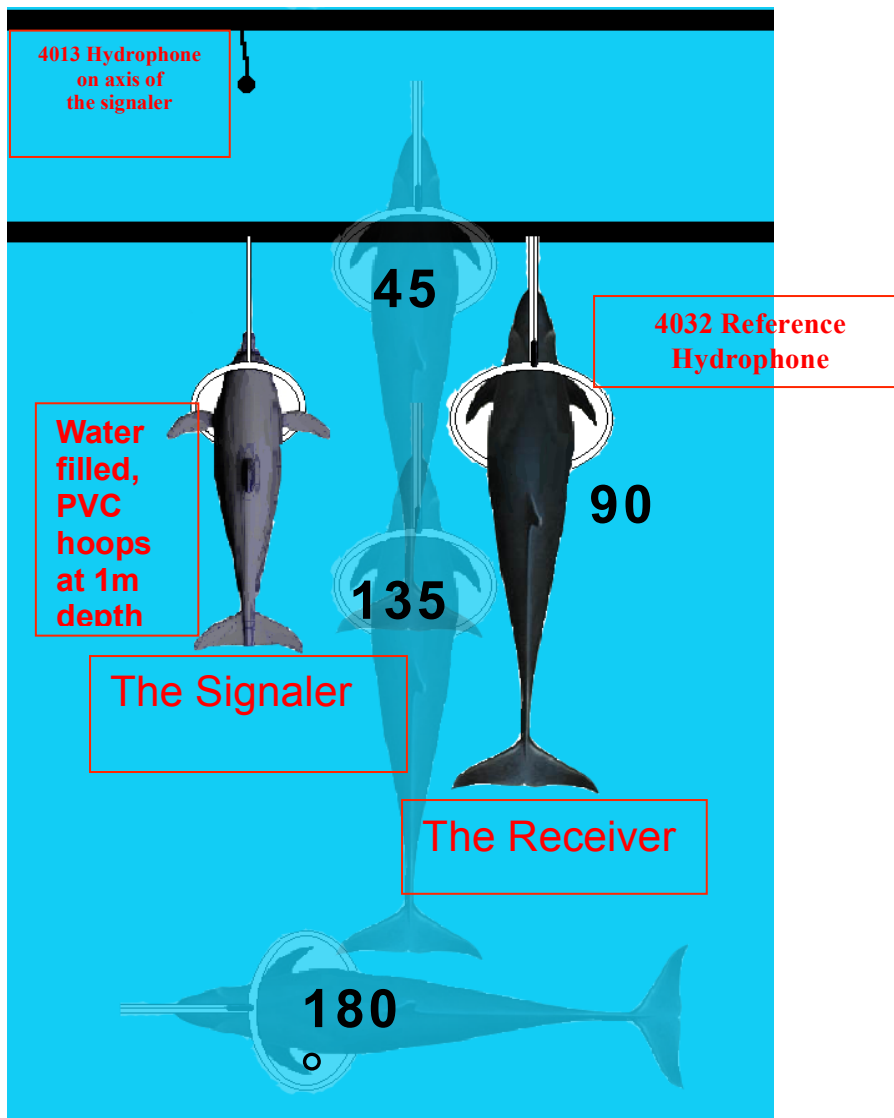


Figure 2. a) DTAG placed on lower left jaw fat. b) DTAG placed on gular area. c) DTAG placed on lower right jaw fat.

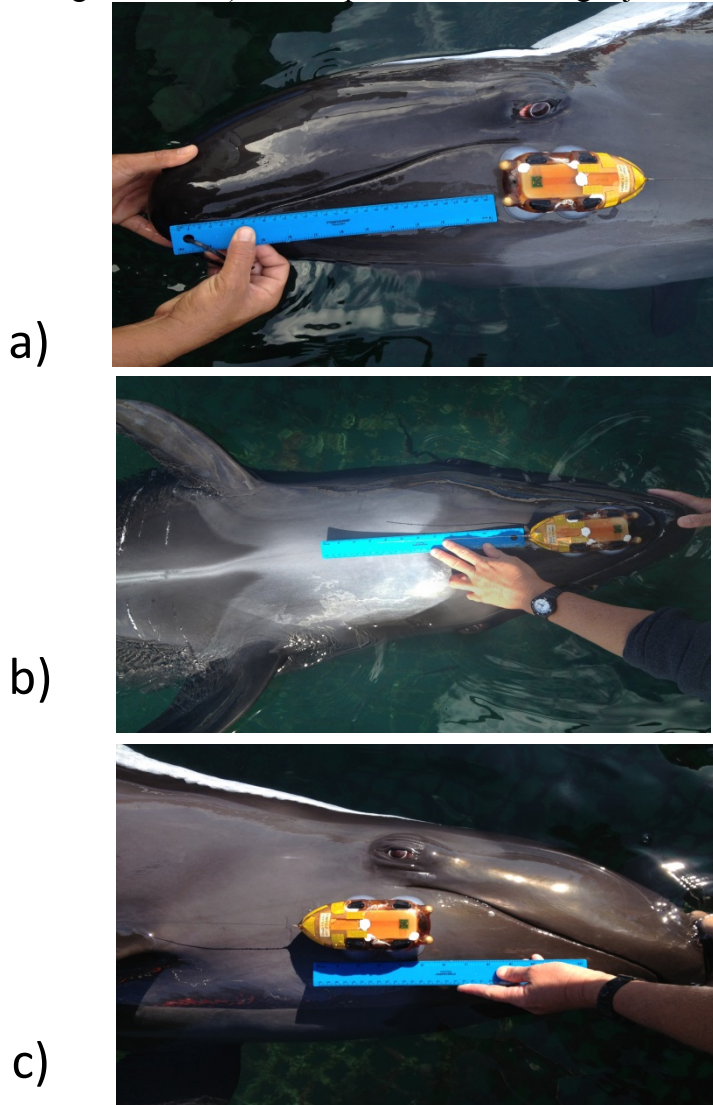


Figure 3. Adobe Audition spectrogram view of 4 sine type whistles from 1 hoop trial prior to each whistle being selected out for individual analysis. Each whistle has 1 fundamental and 1 harmonic frequency whistle contour.

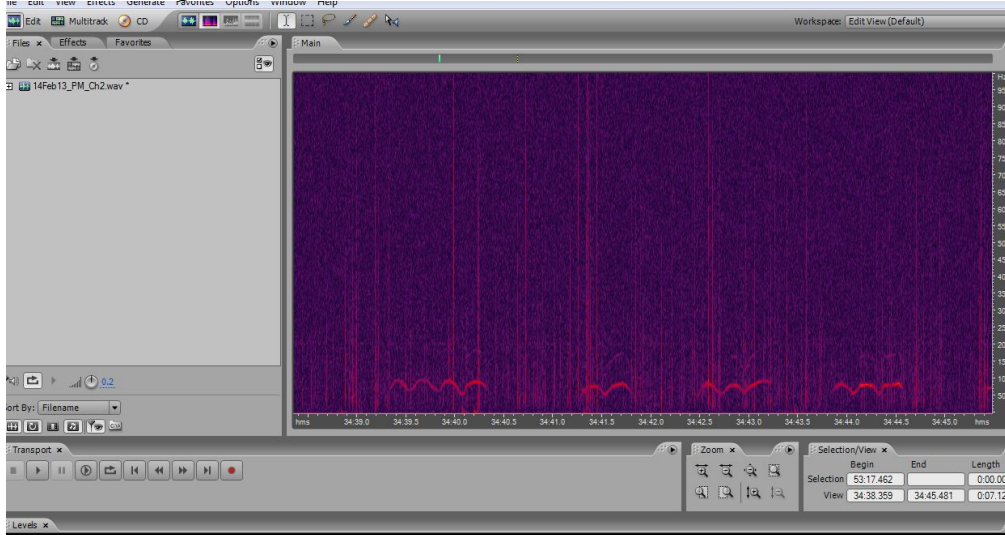


Figure 4. A MATLAB spectrogram view of 1 sine type whistle. The 6 evenly spaced black bars were used for manually selecting points for PSD measurements along the whistle contour where 95% of the energy occurred. There was 1 harmonic frequency contour counted here. High & low-pass filters were also manually selected for each whistle. Snapping shrimp broad-band clicks that overlap the whistle are also clearly visible.

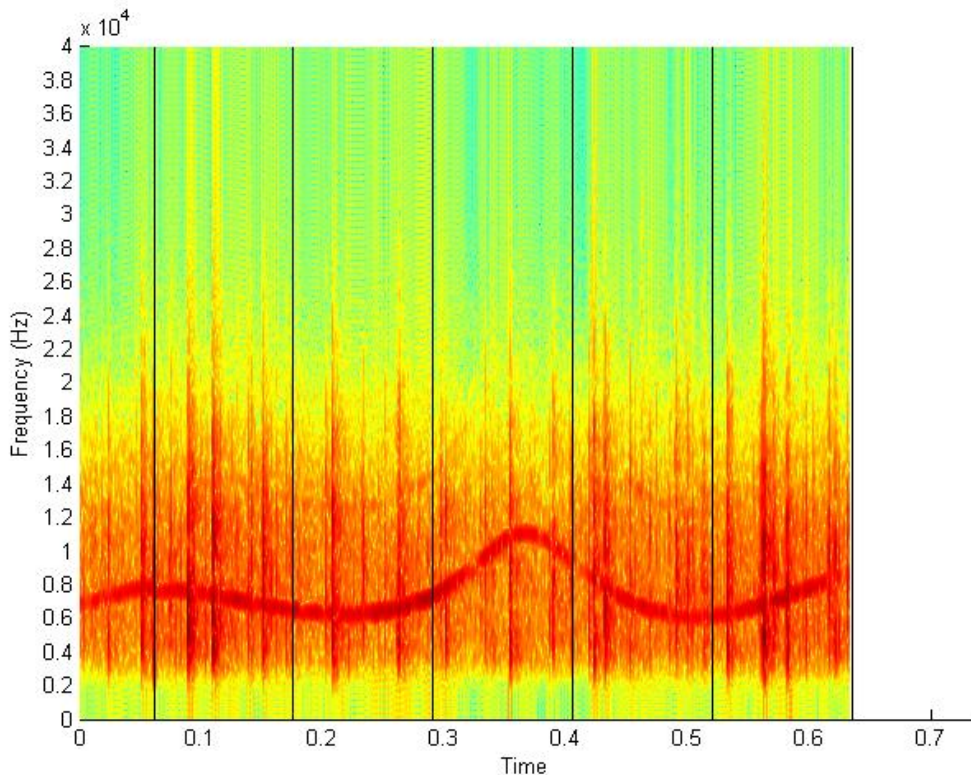


Figure 5. *Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by receiver position as recorded on DTAGs*

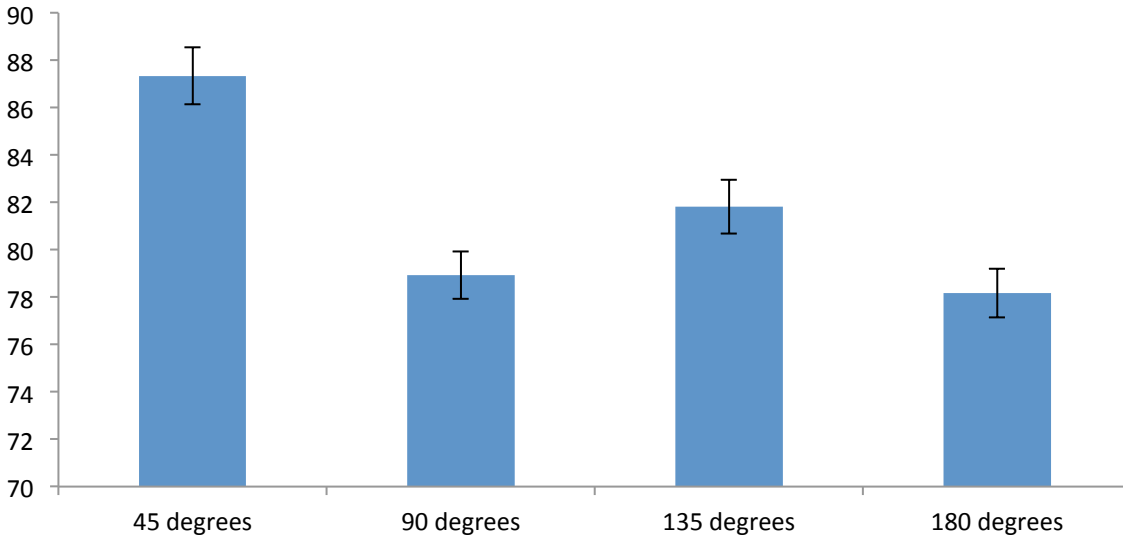


Figure 6. *Estimated Number of Harmonics, ± 1 SE, by receiver position as recorded on DTAGs*

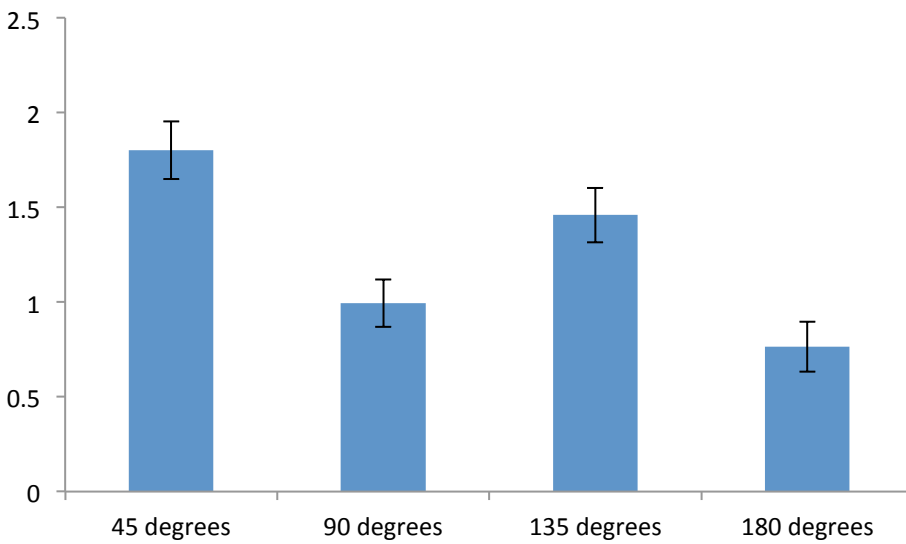


Figure 7. Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement as recorded on DTAGs

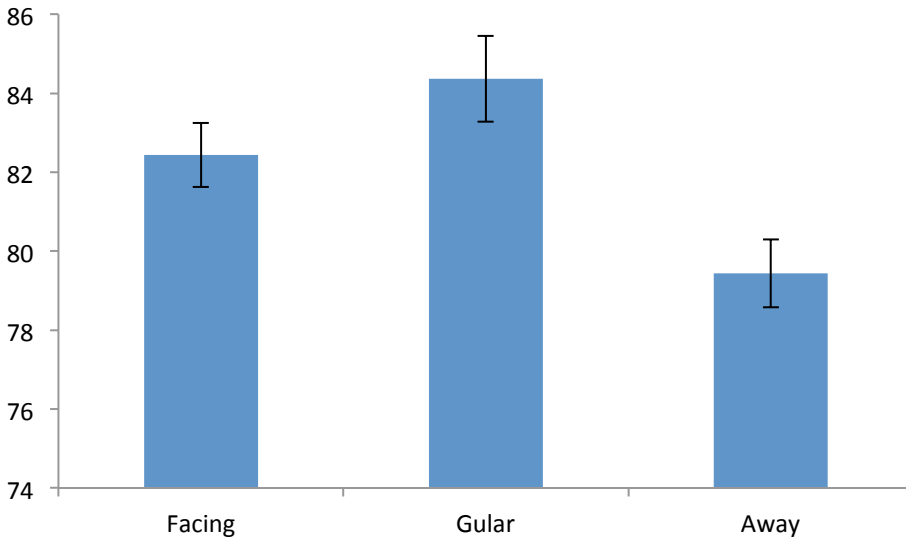


Figure 8. Estimated Mean Number of Harmonics ± 1 SE, by DTAG Placement as recorded on DTAGs

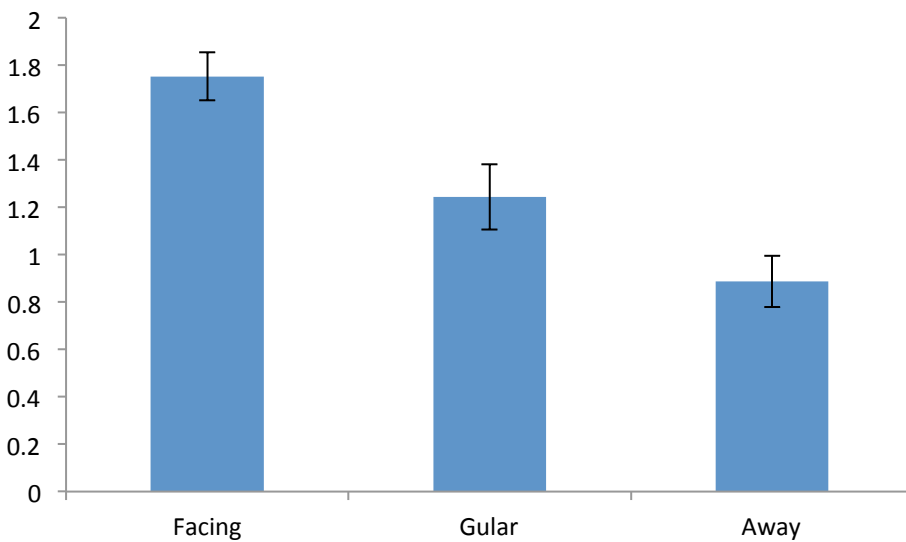


Figure 9. *Estimated Mean Number of Harmonics ± 1 SE, by Interaction of DTAG Placement and Receiver Position as recorded on DTAGs*

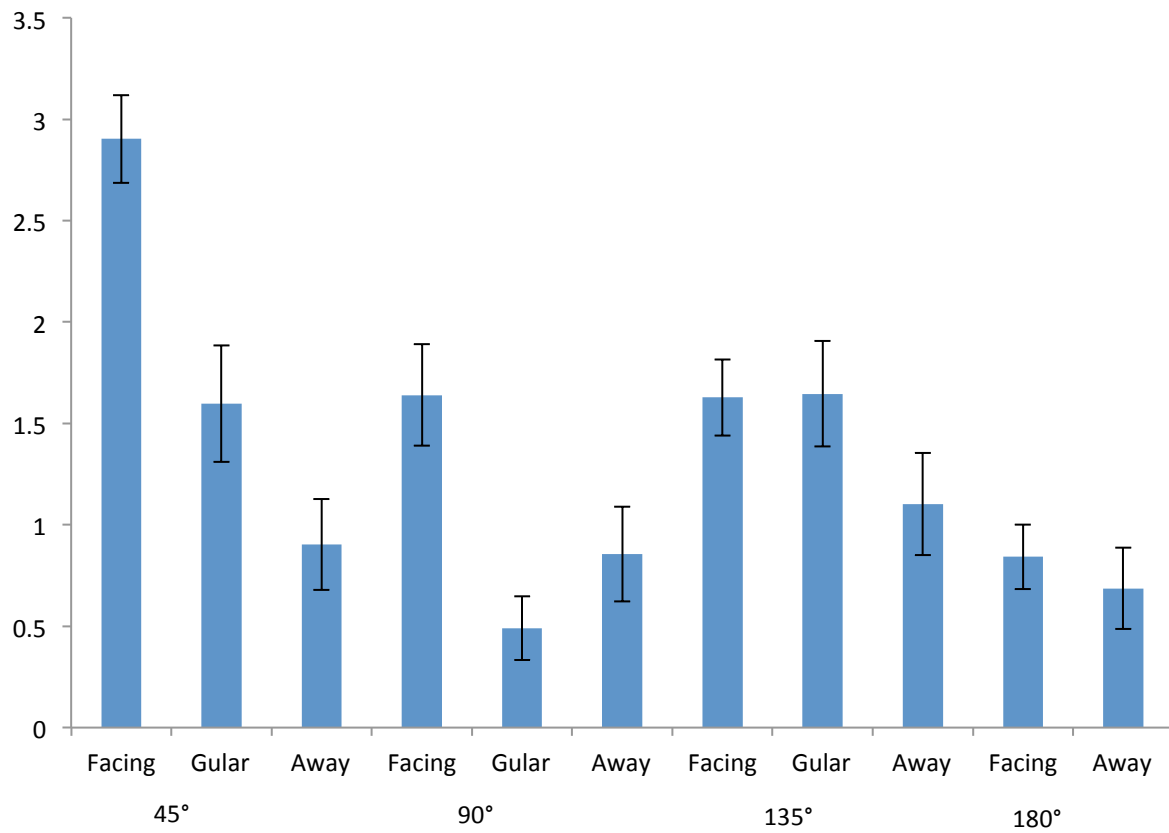


Figure 10. *Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement in the 45° Receiver Position as recorded on DTAGs*

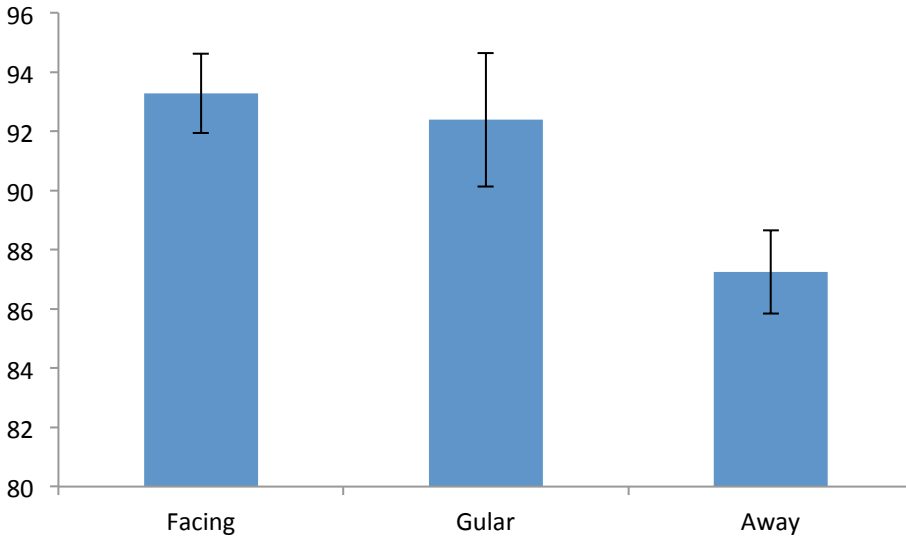


Figure 11. *Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$), ± 1 SE, by DTAG Placement in the 90° Receiver Position as recorded on DTAGs*

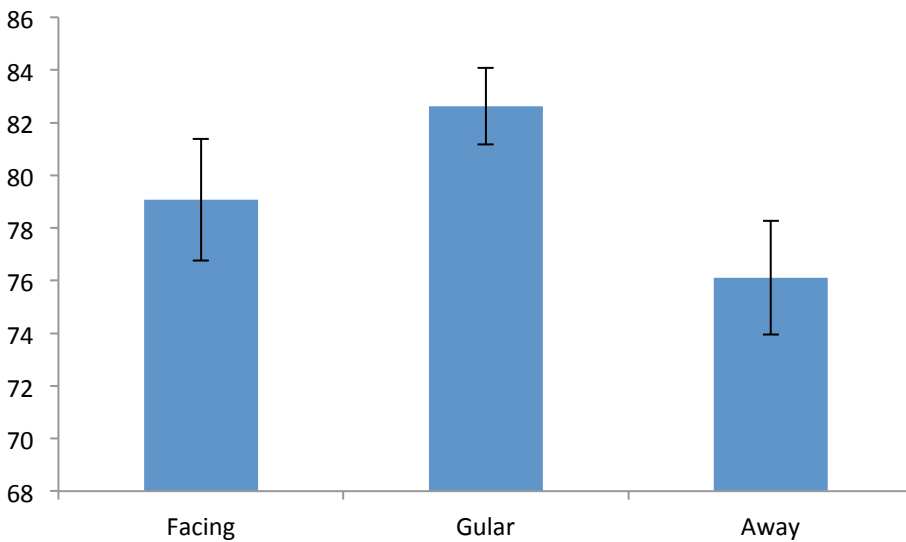
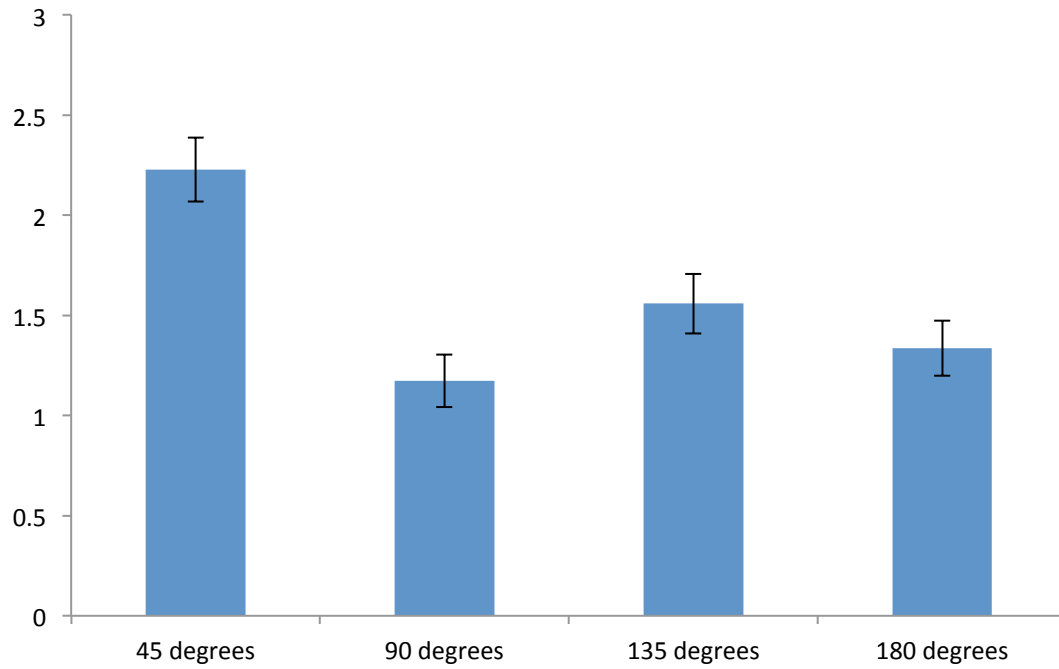


Figure 12. *Estimated Mean Number of Harmonics, ± 1 SE by Position, as measured by the 4032 reference hydrophone, placed above the receiving animal*



TABLE

Table 1. Summary statistics & general characteristics of whistles ($N = 134$) as measured by the DTAG

<i>Location (degrees from signaler) & DTAG placement</i>	<i>n</i>	<i>Duration (seconds) Mean (SD)</i>	<i>Peak Freq. (kHz) Mean (SD)</i>	<i>Min Freq. (kHz) Mean(SD)</i>	<i>Max Freq. (kHz) Mean (SD)</i>	<i>DTAG PSD Mean (SD)</i>	<i>DTAG # of Harmonics Mean (SD)</i>
45°	32	0.64 (0.17)	8.3 (1.4)	5.2 (0.79)	11.3 (1.4)	90.84 (6.19)	2.22 (1.29)
Facing	14	0.58 (0.10)	9.0 (.64)	5.5 (.88)	11.8 (1.6)	94.29 (4.11)	3.29 (.83)
Gular	6	0.72 (0.17)	6.8 (1.8)	5.0 (.46)	10.5 (1.1)	89.01 (4.55)	1.67 (1.21)
Away	12	0.66 (0.21)	8.3 (1.2)	5.5 (.75)	11.2 (1.1)	87.75 (7.15)	1.25 (0.75)
90°	37	0.57 (0.22)	6.1 (1.5)	5.0 (1.1)	10.6 (.90)	80.28 (7.79)	0.86 (0.82)
Facing	8	0.60 (0.11)	6.6 (1.7)	4.8 (1.2)	10.6 (.90)	80.25 (6.35)	1.75 (0.71)
Gular	20	0.50 (0.13)	6.3 (1.4)	5.0 (1.1)	10.8 (.92)	82.19 (9.15)	0.50 (0.61)
Away	9	0.67 (0.35)	5.2 (1.3)	5.0 (1.0)	11.0 (1.0)	76.05 (3.12)	0.89 (0.78)
135°	31	0.58 (0.15)	6.4 (1.3)	5.2 (.59)	10.7 (1.1)	79.57 (3.95)	1.29 (0.69)
Facing	14	0.56 (0.14)	6.7 (1.5)	5.0 (.64)	11.1 (1.3)	80.74 (3.70)	1.57 (0.65)
Gular	8	0.66 (0.19)	6.2 (1.0)	5.1 (.53)	10.4 (.56)	79.74 (4.63)	1.38 (0.74)
Away	9	0.55 (0.15)	6.3 (1.4)	5.4 (.55)	10.2 (.66)	77.59 (3.29)	0.78 (0.44)
180°	34	0.56 (0.22)	6.6 (1.4)	5.7 (.74)	10.0 (.97)	76.58 (6.54)	0.62 (0.74)
Facing	20	0.57 (0.23)	7.1 (1.3)	5.6 (.62)	10.1 (1.0)	78.34 (5.09)	0.75 (0.79)
Away	14	0.54 (0.22)	6.7 (2.1)	5.8 (1.4)	10.1 (2.7)	74.07 (7.71)	0.43 (0.65)

Estimated Mean Power Spectral Density (PSD, in dB re 1 $\mu\text{Pa}^2/\text{Hz}$)

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