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A Description of Vocalizations and Their Association with Mouthing Behaviors and Social Context in Bottlenose Dolphins, *Tursiops truncatus*

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A DESCRIPTION OF VOCALIZATIONS AND THEIR ASSOCIATION WITH

MOUTHING BEHAVIORS AND SOCIAL CONTEXT IN BOTTLENOSE

DOLPHINS, *TURSIOPS TRUNCATUS*

by

Christina Elyse Perazio

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ABSTRACT

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Dolphin communication is multimodal and incorporates physical behaviors and vocalizations. Dolphins often exchange information with conspecifics using different types of vocalizations, and these vocalizations are sometimes associated with specific behaviors. However, the relationship of vocalization type and mouthing behavior type has not been investigated. This thesis examines simultaneous acoustic and visual recordings of bottlenose dolphins (*Tursiops truncatus*) to determine the relationship between type of mouthing behavior and type of vocalization (whistle, whistle-squawk, chirp, moan, burst-pulse type A, burst-pulse type B, and click trains). The role of the social context of a mouthing behavior is also evaluated. Data were obtained opportunistically from a captive population of bottlenose dolphins at the Roatan Institute for Marine Science from March 2010 through June 2011. Raven Pro 1.4 is used to visually code vocalization types during all instances of each of three mouthing behaviors (mouthing, open mouth and bite/rake) and associated social contexts. Burst-pulse 'B' vocalizations are the most frequent. By behavior type, the highest average rate of vocalizations are of whistles during mouthing. By context, the highest average rate of vocalizations are of whistle squawks during aggression. There is a difference in the rate

ii

of three frequency-modulated vocalizations across behavior type.

When the social context of mouthing behaviors is examined, both pulsed and tonal vocalizations differ in rate. There is also a difference in the rate of several types of whistle contours across behavior type. This study is the first to document a change in frequency and type of vocalization with respect to mouthing behaviors and demonstrates that bottlenose dolphin information exchange during mouthing behaviors is organized and fluid with respect to the social environment.

DEDICATION

To my parents-

Moving to Mississippi was a big step, but your love and belief in me never wavered.

Thank you for listening to me cry and scream out of excitement or frustration from

thousands of miles away on the phone, for reading my work, and for always knowing I

could do it.

To Dr. D-

If not for you, I would not be a graduate student right now. You opened my eyes to the

world of animal behavior research and gave me the opportunity to be a part of the

research process early on. You are continually a source of support and inspiration and

have calmed me down from the brink of hysteria at many points. I owe you more than a

"thank you."

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TABLE OF CONTENTS

CHAPTER

   Communication
   Communication in Cetaceans
   Communication in Dolphins
   Current Study

   Subjects and Study Site
   Data Collection
   Data Analysis

   Vocalization Types
   Vocalizations and Behavior
   Vocalizations and Social Context
   Behavior Type and Social Context Interaction
   Whistle Contour
   Whistle Contour and Behavior Type
   Whistle Contour and Social Context
   Mouthing Behaviors in Silence

Vocalizations According to Mouthing Behavior Type
The Role of Social Context
Variations in Whistle Contour
Behaviors in Silence
Study Implications

LIST OF TABLES

Table

viii

LIST OF ILLUSTRATIONS

Figure

CHAPTER I

INTRODUCTION

Studying all animal species in the wild is a vital aspect to understanding their communication systems by identifying the individual units of the system (Kuczaj & Kirkpatrick, 1993). This analysis is accomplished by making observations of natural behaviors (Kuczaj & Kirkpatrick, 1993). This concept is the foundation behind studies of dolphin vocalizations. There are many studies that correlate visual displays and accompanying vocalizations as a means of determining the function of acoustic signals. As these studies are expanded upon in Chapter II, it will become clear that they provide insight into potential differences in the type of information exchanged within a given behavioral or social setting. This association of behaviors and vocalizations has not yet been examined for bottlenose dolphin mouthing behaviors; therefore, the function and significance of mouthing behaviors within social interactions is presently unknown. These findings will allow researchers to make predictions regarding differences in group communication during mouthing behaviors.

CHAPTER II

REVIEW OF RELATED LITERATURE

Communication

Communication, especially intraspecific, is prevalent across the animal kingdom

due to its strong connection to individual fitness. Information is exchanged to benefit

either or both parties (Zimmer, 2011). Communication has, over time, selected for

senders who are able to alter the actions of another while receiving personal gain, and for

receivers who can distinguish crucial verses non-important information from a signal

(Seyfarth & Cheney, 2003). Vauclair (1996) defines communication as a sharing of

various types of information within this signaler-receiver dyad, based on a pre-defined set

of signals. These signals contain information that is different with respect to the

individuals' behavioral state, as well as contextual information surrounding the signal

exchange (Zimmer, 2011). Furthermore, there is a prevalent social component to

communication (Matessi, Matos, Peake, McGregor, & Dabelsteen, 2010; Seyfarth &

Cheney, 2003) as the information exchanged is dynamic and a part of a complex

interaction between individuals (Seyfarth & Cheney, 2003). Therefore, the social

environment in which a communicative event occurs can influence the information that is

transferred.

Communication occurs through a myriad of sensory modalities in different

species, including hormone secretion (grey partridges *Perdix perdix* and plainfin

midshipman *Porichthys notatus*; Oliveira, 2005), specialized dance (honeybees *Apis

mellifera*; Reznikova, 2007), gestures and vocalizations (chimpanzees (no genus, species

listed); Leavens, Russell, & Hopkins, 2010), and vibrations (insect, amphibian, and

mammal species; Hill, 2001). Furthermore, the production of acoustic signals is often influenced by both physical and social environmental factors, such as the relationship of the participating individuals (Seyfarth & Cheney, 2003). For example, lizards use their olfactory system to determine whether a conspecific is familiar or a stranger and modify their aggression levels accordingly (Carazo, Font, & Desfilis, 2008). Behavioral modifications also occur in Siamese fighting fish where males alter their aggressive interactions as a result of audience sex and reproductive state (Dzieweczynski, Earley, Green, & Rowland., 2005) and based on previous experience with a conspecific (Dzieweczynski & Perazio, 2012). Additionally, a signaler may adjust the acoustic properties of vocal emissions to aid the receiver in comprehending the signaler's meaning (Seyfarth & Cheney, 2003). For example, yellow-bellied marmots adjust the number and frequencies of whistles used when a predator is present, most likely to better define the nature and level of danger (Blumstein & Armitage, 1997). Bats have a collection of vocalizations that can be broadband or tonal in nature, and these distinct sounds are emitted as a function of the social setting (Fenton, 1985). Birds change the amplitude of calls depending on the sex of nearby conspecifics (Cynx & Gell, 2004). Meerkats and suricates have specific alarm calls that specify the type of predator (Reznikova, 2007), and vervet monkeys use different calls depending on the type of danger (Seyfarth, Cheney, & Marler, 1980). Transient killer whales that prey upon marine mammals emit less pulsed sounds than resident conspecifics that prey on fish. This change in vocal behavior is a function of prey type, since marine mammals can hear the pulsed calls while fish cannot (Deecke, Ford, & Slater, 2005).

Signalers modify vocalizations to convey signal meaning, and in a variety of species sounds are often repeatedly emitted during a given social or behavioral context to promote the transfer of information. This is not to say that animals limit certain signals to certain situations, but there are relationships between signal types and certain contexts. Bats use different calls during aggressive encounters than in amicable situations (Fenton, 1985). Golden-backed Uakaris alter the duration and frequency of individual call types as a function of the behavioral context, and the call types occurred with different frequency among contexts (Bezerra, Souto, & Jones, 2010). Weddell seal pups call more when they are alone or upon finding their mothers than they do when they are in contact with their mothers; these calls are also longer and have higher frequencies (Collins, McGreevy, Wheatley, & Harcourt, 2011). Sperm whales have different "families" of coda types that are used depending on context, such as feeding, social, or surface behaviors (Frantzis & Alexiadou, 2008). Additionally, coda production from one whale directly determines when a conspecific responds with a coda or codas and the acoustic nature of those codas (Schulz, Whitehead, Gero, & Rendell, 2008). EOD chirps from brown ghost knife fish are an acoustic signal often associated with aggression, and chirp production in these fish is altered by the presence of chirps from conspecifics (Dunlap & Larkins-Ford, 2003). In sum, it is clear that in order to have a true understanding of the function of communication during given contexts, acoustic signals as well as the accompanying behaviors must be studied in conjunction with one another. This contextual understanding is the only way to obtain a complete picture of the animal's methods and purpose of communicating with conspecifics. Additionally, knowledge of the components of

communication (i.e., language) in a given species is necessary to understand the purpose of communication (Kuczaj & Kirkpatrick, 1993).

Communication in Cetaceans

While different species use diverse modes to communicate with conspecifics, cetacean communication occurs primarily through physical and acoustic exchanges (Herman & Tavolga, 1980). Communicative sounds that contain information vary in amplitude and frequency (Zimmer, 2011). The benefit to acoustic signals is that they are useful both over long distances and in close proximity (Herman & Tavolga, 1980). While most acoustic signals cannot target a specific location or individual, this broad signaling does become advantageous in conveying information to a group (Herman & Tavolga, 1980). Additionally, signals may contain a large amount of information, and these signals can be altered quickly in response to situational changes (Herman & Tavolga, 1980). The use of particular acoustic signals depend in part on the social organization of the group. For example, wild dolphins live in fission-fusion societies, meaning that they may have smaller social units that depend on the relationships of individuals present in the group (Connor, Wells, Mann, & Read, 2000). The maintenance of such a dynamic social structure requires constant communication between members of the group, a great deal of which is through acoustic signaling. Cetaceans may exchange information in order to alter the decision of another conspecific or to share information about the environment (Tyack, 2000). Sperm whales stage their vocal emissions to correlate with conspecific vocalizations as a part of a pair, with the receiver utilizing the vocal of the sender in the timing of their vocal (Schulz et al., 2008). These authors argue that the vocal emission patterns of single whales and pairs of whales suggest that this exchange is not simply due

to an environmental response (Schultz et al., 2008). Given the definition of communication as a sharing of information between a signaler and a receiver (Vauclair, 1996), this example demonstrates signal exchange with a communicative function. Moreover, the social context in which the communication event occurs is important. For example, dolphins emit more low frequency narrow-band calls in group situations where there is an amplified amount of social activity, including sexual interactions, than in non-social situations (Simard et al., 2011). While this research is not conclusive that the vocalizations are emitted as a result of behavioral context, the association suggests the possibility that individual dolphins are emitting certain vocalization types more often in one context compared to another.

Communication in Dolphins

Vocalizations

Across species, bottlenose dolphin (*T. truncatus*) vocalizations are among the most studied (Tyack & Clark, 2000). Their catalogue of vocalizations includes a wide and flexible range of vocalizations (Janik, 2009). Dolphins emit both tonal and pulsed vocalizations (Tyack & Clark, 2000). Burst-pulse sounds are comprised of a series of clicks (Janik, 2009), distinguishable by their repetition rate (dos Santos, Caporin, Moreira, Ferreira, & Coelho, 1990) or inter-pulse interval (Murray, Mercado, & Roitblat, 1998; Watkins, 1968). These sounds have highly variable amplitude and rate, resulting in different but distinct sounds (Popper, 1980). Frequency modulated sounds, including whistles, have tonal distinctions (Simard et al., 2011). Multiple studies document burst-pulse sounds with overlapping whistles, termed a whistle-squawk (Herzing, 1996; Killebrew, Mercado, Herman, & Pack, 2001). Shorter toned sounds that span a large

frequency range have been termed chirps (Caldwell & Caldwell, 1968; Driscoll as cited in Bazúa-Durán & Au, 2002). Similarly, frequency modulated sounds of extremely low frequencies are called moans (van der Woude, 2009). In addition to understanding the types of vocalizations, researchers tend to study sounds within the surrounding social environment, as behavior has been shown to relate to sound in a variety of species.

Vocalizations, Behavior, and Context

Studies with dolphins have examined the relationship between the behavioral repertoire and acoustic signals (Herzing, 2000) for a variety of sounds. It is important to understand, however, that vocalizations are not mutually exclusive to certain behavior types. Still, it is not uncommon for individuals to associate certain sounds repeatedly within a behavioral context at a given time. Aggressive contexts are sometimes associated with burst-pulse sounds (Blomqvist & Amundin, 2004) or with whistle squawks (Herzing, 1996). Alternatively, whistle squawks are heard during sexual play (Herzing, 1996). "Pop" sounds are heard simultaneously with sharp and fast head movements (Connor & Smolker, 1996) and may also be in association with aggression. Whistles are heard more frequently during socializing than traveling behavioral states (Hernandez, Solangi, & Kuczaj, 2010; Quick & Janik, 2008), and more specifically, are heard during instances of aggression, play behaviors and conspecific rubbing (Dudzinski, 1998). Other dolphins engaging in play-fight behaviors emit a characteristic burst sound trailed by a whistle, which is not heard during aggressive behaviors (Blomqvist, Mello, & Amundin, 2005). Signature whistles are heard during mother, or other female, and calf interactions (Herzing, 1996). Several vocalization types are heard in association with human interactions, including variants of pulsed sounds and whistles (Herman &

Tavolga, 1980). Click trains, squawks, and whines are heard as individuals explore an area (Dudzinski, 1998), and clicks are also heard during both foraging behaviors and social contact (Van Parijs & Corkeron, 2001).

Additionally, individuals may modify features of a specific vocalizations with respect to behavior. For example, dolphins may alter whistle parameters such as duration, frequency, or strength as context changes (Herman & Tavolga, 1980; Lopez, 2011). Specifically, individual dolphins emit less whistles in larger groups (Hawkins & Gartside, 2010; Quick & Janik, 2008). Above findings exemplify the usage of certain vocalizations across contexts and also demonstrate that dolphins use a variety of sounds in any given context.

For dolphins, the literature on types of vocalizations recorded during any given behavioral setting associated context is important in understanding the use of acoustic signals during conspecific communication. The use of diverse vocalization types between and among contexts is indicative of communicative flexibility. Altering responses based on situational and behavioral circumstances defines flexible communication (Kuczaj & Makecha, 2008). If dolphins actively alter signal types as a result of behavioral state, social context, or the presence of other individual, there may be support for the suggestion that vocalizations have significance in communication.

Mouthing displays

There are three types of mouthing behaviors referenced in the dolphin literature: biting or raking, open mouth displays, and mouthing. Biting and raking (see Appendix A for definitions) often involve an aggressive or threatening intent (Dudzinski, 1998; Herman & Tavolga, 1980; Holobinki & Waring, 2010; Scott, Mann, Watson-Capps,

Sargeant, & Connor, 2005; Shane, Wells, & Würsig, 1986). Rake marks on conspecifics are linked to fighting and mouthing displays (Lockyer & Morris, 1985). Open mouth displays (see Appendix A for definitions) are also observed in antagonistic social environments involving bottlenose dolphins (Overstrom, 1983) and are often indicative of fighting or aggression (Holobinki & Waring, 2010; Samuels & Gifford, 1997). Mouthing (see Appendix A for definitions) is often exhibited by captive males during mating attempts (Saayman, Tayler, & Bower, 1973; Shane et al., 1986). Additionally, mouthing, unlike open mouth or biting/raking, has been observed in non-aggressive environments (Kuczaj & Yeater, 2007). Little is known about the relationship between social context and mouthing behavior. However, Seay, Levengood, Gross, Dudzinski, and Kuczaj (2011) found that mouthing events occur during six social contexts: aggressive, herding, orient, socio-sexual, social and swim by. Assessing the vocalizations during mouthing behaviors, which are not limited to a single context, will add to the literature on how dolphins use sound during interactions.

Current Study

This study investigates the possibility that vocalizations vary depending on the type of mouthing display (open mouth, mouthing, biting/raking-see Appendix A for definitions), and the corresponding possibility that specific combinations of vocalizations and mouthing displays may communicate different information to other dolphins. This requires that the social setting of the mouthing behavior be taken into consideration. Social contexts may involve aggression, herding, orienting, socio-sexual behaviors, non-aggressive social behaviors, and swim-by instances (see Appendix B for definitions). This research was developed from prior research that has found variations in vocalization

type with respect to behavioral category and social context (Blomqvist et al., 2005;

Connor & Smolker, 1996; Dudzinski, 1998; Fenton, 1985; Herman & Tavolga, 1980;

Herzing, 1996; Quick & Janik, 2008; Schultz, Cato, Corkeron, & Brydon, 1995; Van

Parijs & Corkeron, 2001).

CHAPTER III

METHODOLOGY

Subjects and Study Site

Dolphins housed at the Roatan Institute for Marine Science (RIMS) at Anthony's Key Resort in Roatan, Bay Islands, Honduras between March of 2010 and June of 2011 were the subjects of this study. According to Dudzinski, Gregg, Melillo-Sweeting, Seay, Levengood, and Kuczaj (2012), the dolphins at RIMS maintain a group structure that is similar in age and sex organization to wild dolphin populations in Shark Bay, Australia (Connor, Mann, & Watson-Capps, 2006) and Mikura Island, Japan (Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004). This similarity makes generalizations from the captive population at RIMS to wild bottlenose dolphins reasonable. The population at RIMS during data collection included twenty-four dolphins: 13 males (four adults, two sub-adults, four juveniles and three calves) and 11 females (seven adults, three juveniles and one calf). The dolphins were housed in a $300m^2$ enclosed natural lagoon that reaches a depth of eight meters. This lagoon is characterized by a bottom of sand, coral, and sea grass beds (Figure 1).

Data Collection

Simultaneous video and audio recordings of underwater behaviors and accompanying vocalizations were taken opportunistically from March 2010 to June 2011, culminating in 20 minutes and 22 seconds of recorded mouthing displays. Data was collected by Stan Kuczaj using a Cannon 7D with Tokina 2.8 11-16mm lens and a Nauticam underwater housing with hydrophone.

Figure 1. The Roatan Institute for Marine Science in Anthony's Key, Roatan, Honduras.

These data were also used by Seay et al. (2011) to assess type of mouthing display, duration of the behavior, when the behavior occurred (date and time) and the context during which the mouthing display occurred. Mouthing displays were coded as mouthing displays, biting/raking behaviors, or open mouth events directed towards a conspecific (Seay et al., 2011). Definitions for these behaviors in the current study were adapted from Seay et al. (2011) (Appendix A). Social contexts were coded as aggressive, herding, orient, socio-sexual, social, and swim-by contexts (Seay et al., 2011). Definitions for these contexts in the current study were adapted from Seay et al. (2011) (Appendix B).

Data Analysis

Acoustic recordings were extracted as .mov files from the videos, and spectrograms were generated using the Raven Pro 1.4 Interactive Sound Analysis Software, developed by the Cornell Lab of Ornithology. Spectrogram parameters were set to remain stable throughout analysis: window type Hann with 1200 samples window size, 50% overlap 600 samples hop size, and 3db filter bandwidth. Due to the equipment used for data collection, individual vocalizations could not be paired with specific dolphins. Therefore, all vocalizations during each behavioral instance were analyzed. All instances of mouthing displays between March of 2010 and June of 2011 were identified within the data set and coded for the presence and number of each type of vocalization and whistle contour. Mouthing displays that occurred in silence were also included in the analysis to serve as a point of comparison to those that did involve sound. Inter-observer reliability for the coding of vocalization types and whistle contour was obtained using 20% of the data. Both coders reached 80% reliability for each vocalization type and each contour. Vocalization types for the analysis included the following: whistle, whistle squawk, chirp, moan, burst-pulse type A, burst-pulse type B, and click trains. These vocalization categories were chosen based on their consistent use in previous literature. Burst-pulse vocalizations were coded visually from the spectrograms created in Raven. Burst-pulse sounds and clicks were additionally coded using the inter-pulse intervals (IPI) of peaks in amplitude within each pulsed sound to determine the IPI ranges for each vocalization category. This process was double-checked using a second blind researcher who pulled sample vocalizations to be coded based on their IPI. Ranges of IPIs for burst-

pule type A, burst-pulse type B, and click trains were included with the visual definitions

for each sound category (Table 1).

Table 1

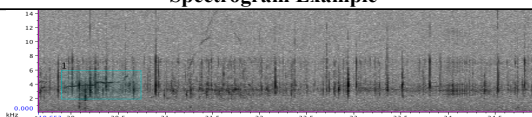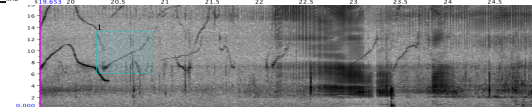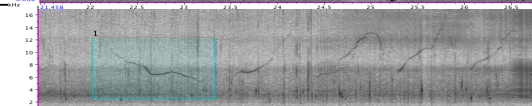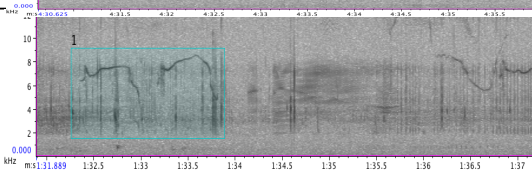*Vocalization Type Definitions, Spectrogram Examples, and References*

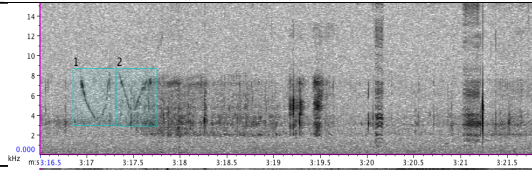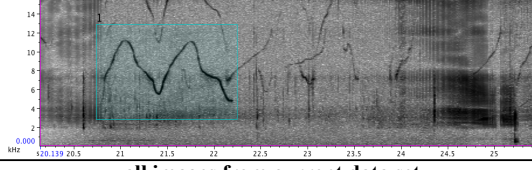| Type	Definition	Spectrogram
Whistle	Narrowband, frequency modulated (Herzing, 1996) sounds having tone (Caldwell & Caldwell, 1968). Whistles counted individually if consecutive whistles separated by >.03 seconds (Gridley, Berggren, Cockcroft, & Janik, 2012) or not continuous from end of whistle A to start of whistle B.	
Whistle-squawk	Whistle with broadband burst pulse characteristics during some duration of the whistle (Herzing, 1996; Killebrew, Mercado, Herman, & Pack, 2001). Counted separately for each whistle/burst pulse involved.	
Chirp	Brief and pure tone (Caldwell & Caldwell, 1968) whistle less than .3sec in duration (Driscoll, A. D., 1995 (as cited in Bazúa-Durán & Au, 2002) that covers a range of frequencies, often upsweep (Caldwell & Caldwell, 1968).	
Moan	Sounds with modulated fundamental frequencies less than .5khz (van der Woude, 2009) of differing duration.	
Burst-pulse type A	A broadband, wideband vocalization (Killebrew et al., 2001) with clear horizontal bars, visibly separated by white space on the spectrogram. Inter-pulse interval below .009 seconds.	
Burst-pulse type B	A broadband, wideband vocalization (Killebrew et al., 2001) that appears patterned or blurred on a spectrogram. Inter-pulse interval between .010 seconds and .019 seconds.	
Click train	Definitive, short, broadband (Killebrew et al., 2001) sounds (vertical lines on spectrogram) that are repeated rapidly. Inter-pulse interval above .020 seconds.	
Other	Sound that does not fit into above categories.	N/A
	see individual references cited within definitions	**all images from curent study data**

Whistles were further divided into categories based on contour (Table 2) to assess any differences in the shape of whistles between behavior types or contexts.

Table 2

*Whistle Contour Definitions and Examples*

Contour Name	Spectrogram Example	Definition
Constant		Less than 1kHz difference in frequency throughout the entire whistle. This frequency range is less than a fourth of the whistle duration. Bazúa-Durán & Au, 2002.
Upweep		Increase in frequency, with the frequency change in any inflection point making up less than half of the whistle's frequency range. Bazúa-Durán & Au, 2002.
Downsweep		Decrease in frequency, with the frequency change in any inflection point making up less than half of the whistle's frequency range. Bazúa-Durán & Au, 2002.
Convex		One inflection point at minimum, beginning with an increase in frequency followed by a decrease. The increasing and decreasing sections of the whistle make up more than half of the whistle's frequency range. Bazúa-Durán & Au, 2002.
Concave		One inflection point at minimum, beginning with a decrease in frequency followed by an increase. The increasing and decreasing sections of the whistle make up more than half of the whistle's frequency range. Bazúa-Durán & Au, 2002.
Sine		Two inflections points at minimum, with an increasing-decreasing patterns to the contour. Must be at minimum 3 of these contours within the single whistle making up more than half of the whistle's frequency range. Bazúa-Durán & Au, 2002.
	all images from current data set	

The emission rate of each type of vocalization and whistle contour was compared across behavior types and across social contexts using analyses of variance. All statistics were run using IBM SPSS version 21.

CHAPTER IV

ANALYSIS OF DATA

Vocalization Types

A total of 677 observed mouthing behaviors were included in the analysis. Figure 2 depicts the frequency of mouthing behaviors across social contexts. Open mouth behaviors (N=629) account for 93% of the observed behavioral instances (Figure 2). Open mouth displays (N=249) occurred most often during the non-aggressive social context (Figure 2). While open mouth displays were seen during all social contexts, mouthing was absent in orient, herding, and swim by contexts, and bite/rake behaviors were absent during herding and swim by contexts (Figure 2). It is of note that both herding and swim by contexts were only characterized by open mouth behaviors (Figure 2).
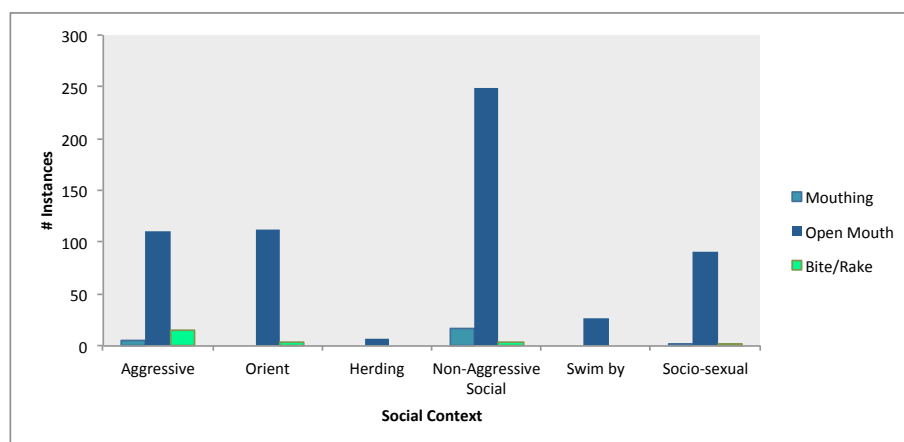
Figure 2. The Total Number of Instances of Each Behavior Type (Mouthing, Open Mouth, Bite/Rake) According to Social Context.

A total of 1377 vocalizations during mouthing behaviors were analyzed. Burst-pulse 'B' (N=390) were the most frequent vocalization type, constituting 28% of all vocalizations, followed by whistle squawks (N=383) and whistles (N=290) (Figure 3).

Moans (N=6) were the least frequent vocalization, accounting for less than 1% of

vocalizations (Figure 3).
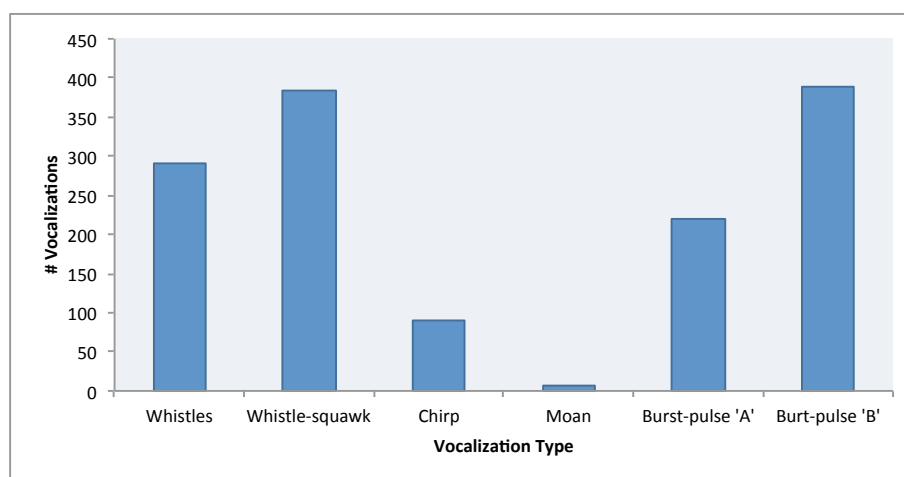
Figure 3. Vocalization Rate According to Type.

Echolocation clicks were counted as present or not present during behavioral

instances. Clicks were present in 31% of all behavioral events of concern (Figure 4).
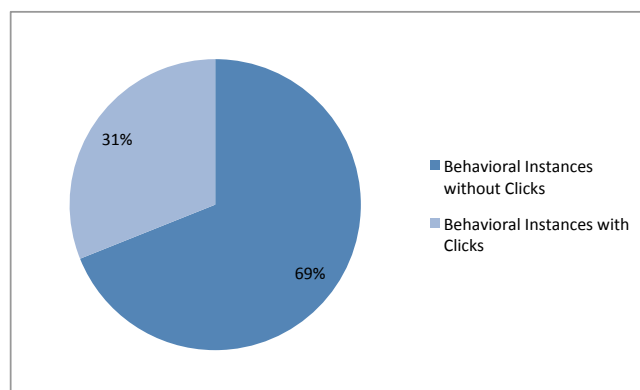
Figure 4. The Percentage of All Behavioral Instances During Which Echolocation Clicks Were Present.

Vocalizations and Behavior

On average, mouthing instances (M=3.79, SD=2.21) were longer in duration than

either open mouth displays or biting/raking (Figure 5). However, looking at the standard

error bars, it is evident that there was much more variation in the duration of mouthing

instances compared to either other behavior type (Figure 5). While open mouth displays
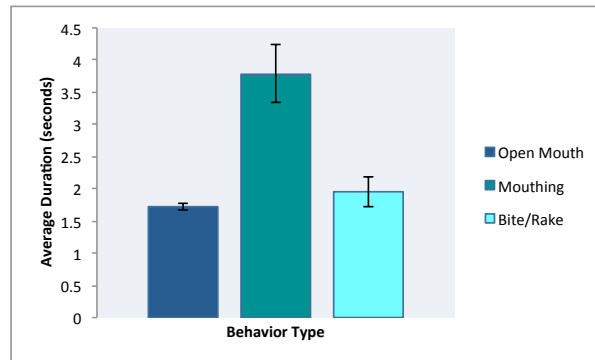
(M=1.72, SD=1.31) had the shortest average duration, they also varied the least (Figure

5). Therefore, the following analyses of vocalizations per mouthing event were not

substantially affected by differences in behavior type duration.

Figure 5. Average Duration of Each Type of Mouthing Behavior.

Mean vocalization rates were used for all comparisons to account for differences

in the sample size of instances of each type of behavior. When the maximum average

vocalization rates were compared across behavior types, instances of mouthing had the

most vocalizations, with whistles (M=1.42, SD=1.67) constituting the majority of

vocalizations (Figure 6a). When the minimum average vocalization rates were compared

across behavior types, instances of biting/raking had the least vocalizations, with no
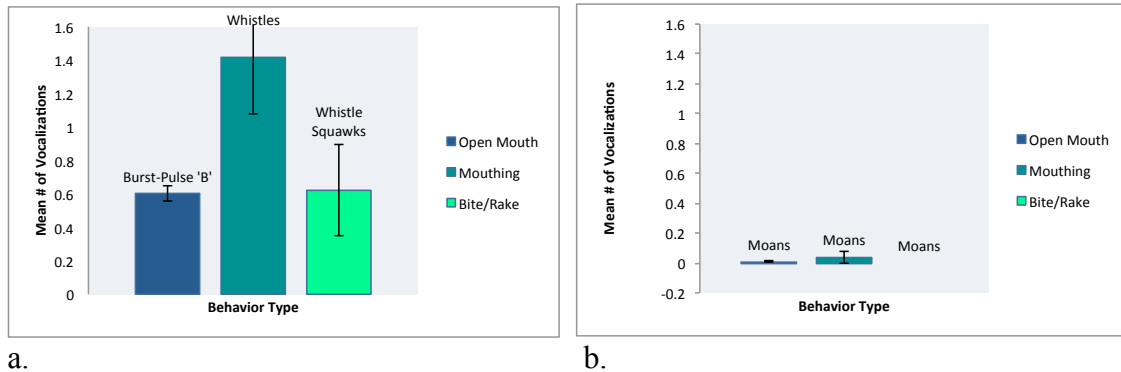
moans present (Figure 6b).

a.　　　　　　　　　　　　　　　　　　　　　　b.

Figure 6. The Maximum (a) and Minimum (b) Average Vocalization Rates Across Behavior Type.

Multivariate Analysis of Variance (MANOVA)

Using Pillai's trace, there was a relationship between behavior type and vocalization rate, $V=0.10$, $F_{(14,1338)} = 4.75$, $p < .05$.

Discriminant Analysis (DA)

The MANOVA was followed up with a discriminant analysis, which yielded two discriminant functions. The first function had canonical $R^2 = .09$, and the second had canonical $R^2=.01$. Together both functions significantly differentiated the behavior types, $\Lambda = .91$, $\chi^2(14) = 66.16$, $p <.05$. Whistles ($r = .67$) and chirps ($r =.62$) differentiated mouthing from both open mouth and bite/rake on function one.

Univariate Analyses of Variance (ANOVA) and Post-Hoc Tests

The MANOVA was followed up with univariate ANOVAs. There was a significant relationship in whistle rate across behavior type, $F_{(2,674)}=14.29$, $p < .05$, and in the rate of chirps across behavior type, $F_{(2,674)}=12.22$, $p < .05$. The relationship for the rate of whistle-squawks across behavior type approached significance, $F_{(2,674)}=2.91$, $p=.055$. The remaining vocalization types did not show a difference in rate according to behavior type. The post-hoc analysis using Tukey's HSD revealed more whistles (Figure

7a) during mouthing compared to open mouth (*p*=.000) and more whistles during mouthing compared to bite/rake (*p*=.000); more whistle squawks (Figure 7b) during mouthing compared to open mouth (*p*=.044); and more chirps (Figure 7c) during mouthing compared to open mouth (*p*=.044) and more chirps during mouthing compared to bite/rake (*p*=.002).

a.

b.

c.
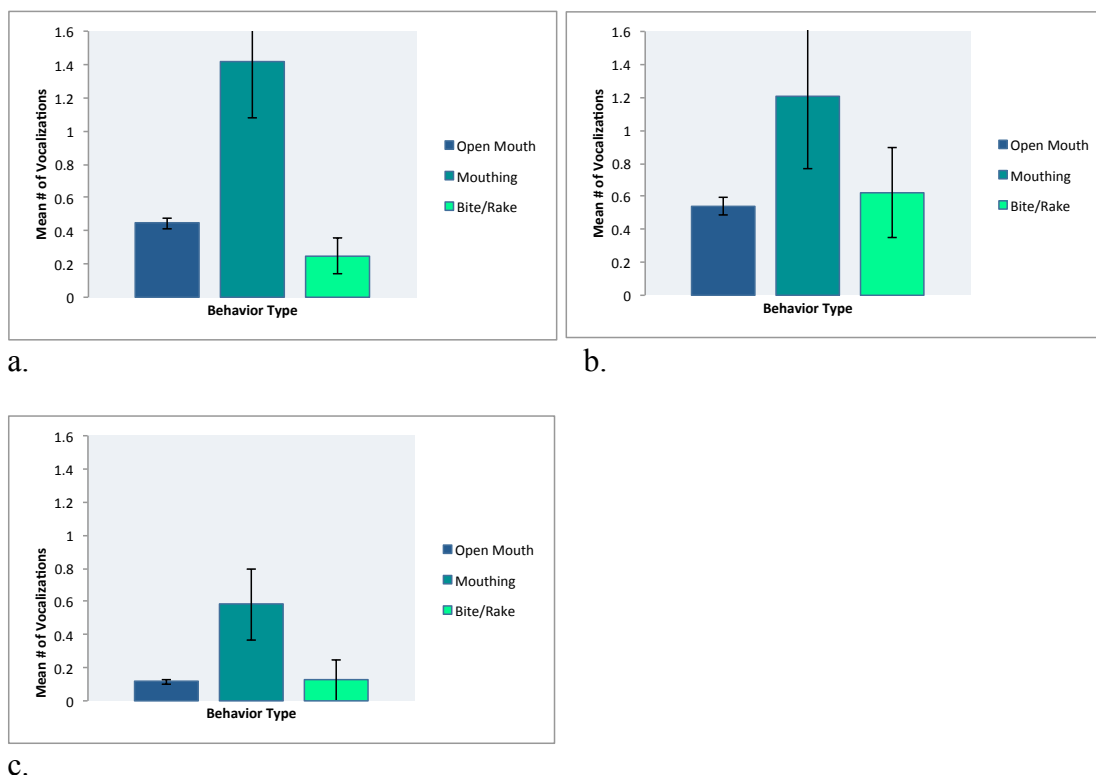
Figure 7. Significant Differences, Illustrated in Post Hoc Comparisons, in the Average Number of Whistles Across Behavior Type (a), Whistle Squawks Across Behavior Type (b), and Chirps Across Behavior Type (c).

Vocalizations and Social Context

When the maximum average vocalization rates were compared across contexts, instances involving aggression had the highest average rate of vocalizations with whistle squawks (M=1.3, SD=2.01) accounting for the majority of vocalizations (Figure 8a). Across contexts, instances involving herding and swim by contexts had the lowest

average vocalization rate, with no whistle squawks, chirps, or moans during herding

contexts and no moans during swim by contexts (Figure 8b).

a.

b.
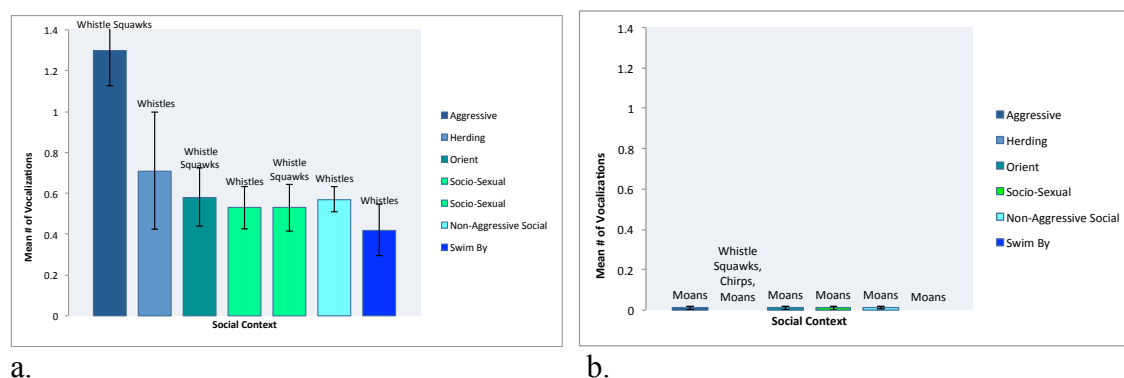
Figure 8. The Maximum (a) and Minimum (b) Average Vocalization Rates Across Social Context.

Multivariate Analysis of Variance (MANOVA)

Using Pillai's trace, there was a significant relationship between social context

and vocalization rate, $V=0.21$, $F_{(42,4014)} = 3.42$, $p < .05$.

Discriminant Analysis (DA)

The MANOVA was followed up with a discriminant analysis, which yielded six

discriminant functions. Function one had canonical $R^2 = .16$, and together all six

functions together significantly differentiated the contexts, $\Lambda = .80$, , $\chi^2(42) = 148.92$,

$p=.000$. Burst-pulse type B ($r =.69$) and whistle-squawks ($r = .67$) differentiated

aggressive from other contexts on function one.

Univariate Analyses of Variance (ANOVA) and Post-Hoc Tests

The MANOVA was followed up with univariate ANOVAs. There was a

significant relationship in whistle rate across context, $F_{(6,670)}=2.30$, $p < .05$, in the rate of

whistle-squawks across context, $F_{(6,670)}=10.00$, $p < .05$ and in the rate of burst-pulse type

B across context, $F_{(6,670)}=10.76$, $p < .05$. The post-hoc analysis using Tukey's HSD

revealed significantly more whistles (Figure 9a) during non-aggressive social compared to aggressive (p=.019); more whistle-squawks (Figure 9b) during aggressive compared to orienting (p=.000), more whistle squawks between aggressive compared to socio-sexual (p=.000), more whistle squawks during aggressive compared to non-aggressive social (p=.000) and more whistle squawks during aggressive compared to swim-by (p=.002) contexts; more burst-pulse-type A (Figure 9c) during non-aggressive social compared to aggressive (p=.042); and more burst-pulse-type B (Figure 9d) during aggressive compared to orienting (p=.000), more burst-pulse type B during aggressive compared to socio-sexual (p=.000), more burst-pulse type B during aggressive compared to non-aggressive social (p=.000) and more burst-pulse type B during aggressive compared to swim by (p=.002) contexts. Neither chirps nor moans were shown to differ in rate based on social context.

a.

b.

c.   d.
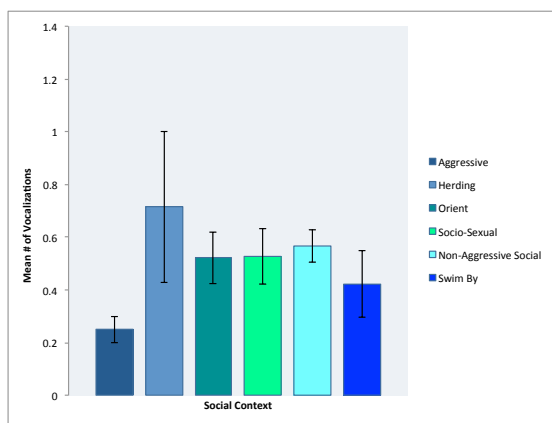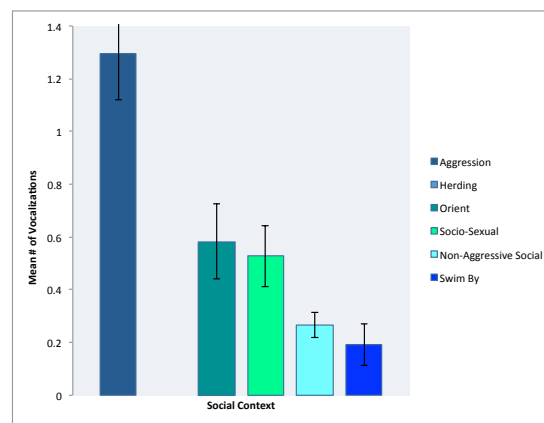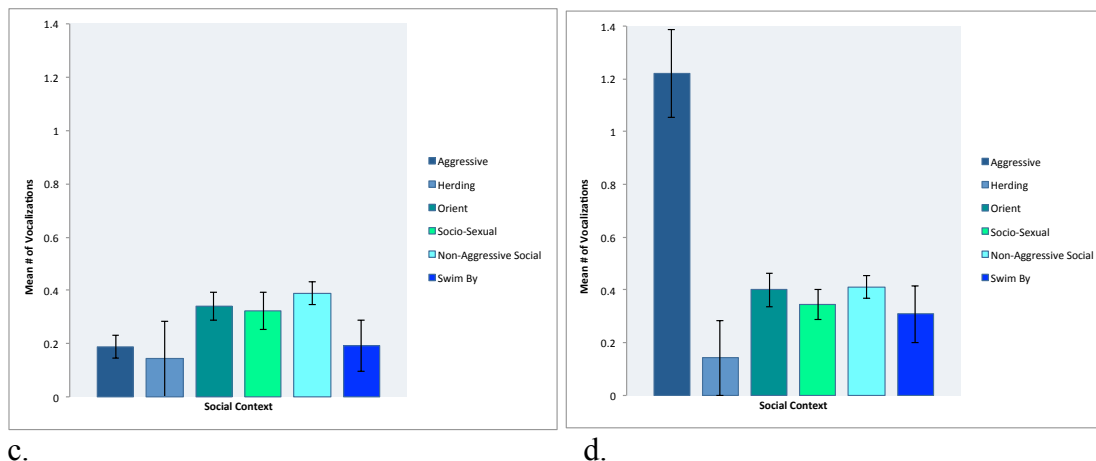
Figure 9. Significant Differences, Illustrated in Post-Hoc Comparisons, in the Average Number of Whistles Across Context (A), Whistle Squawks Across Context (B), Burst-Pulse 'A' Across Context (C), and Burst-Pulse 'B' Across Context (D).

Behavior Type and Social Context Interaction

A factorial multivariate analysis of variance (MANOVA) was run for both behavior type and social context as a comparison of means. However, the descriptive results for this analysis displayed inadequate sample sizes for each individual comparison, indicating that assessing any possible interactions between behavior type and social context is not viable for the current data set.

Whistle Contour

All whistles were coded according to contour (see Table 2 for definitions and examples). Upsweep whistles (N=98) were the most common whistle contour and accounted for 34% of whistles, followed by convex whistles (N=84) (Figure 10). Constant whistles (N=17) were the least common whistle contour, accounting for only 6% of whistles (Figure 10).
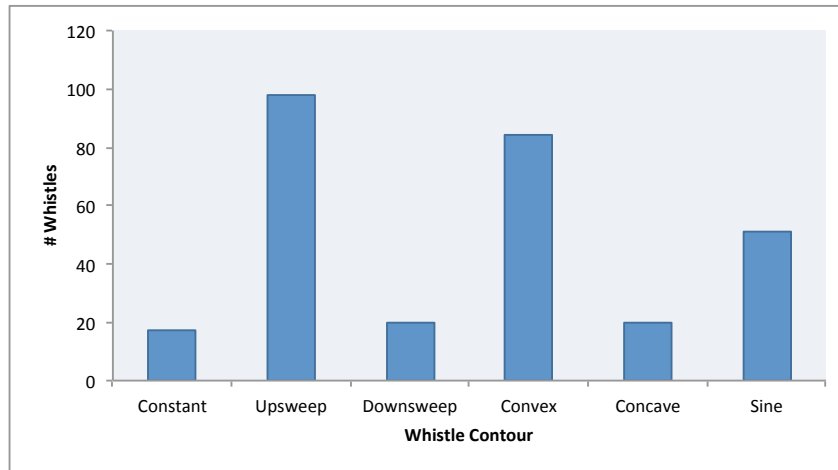
Figure 10. Whistle Rate According to Contour (Shape).

<div align="center">Whistle Contour and Behavior Type</div>

Multivariate Analysis of Variance (MANOVA)

Using Pillai's trace, there was a significant relationship between behavior type and whistle contour rate, $V=0.10$, $F_{(12, 1340)} = 5.85$, $p < .05$.

Discriminant Analysis (DA)

The MANOVA was followed up with a discriminant analysis, which yielded two discriminant functions. Function one had canonical $R^2 = .07$, and function two had canonical $R^2 = .03$. Functions one and two together significantly differentiated the behavior types, $\Lambda = .90$, $\chi^2(12) = 68.75$, $p=.000$, as did function two alone, $\Lambda = .97$, $\chi^2(5) = 22.83$, $p=.000$. On function one, convex whistles ($r = .68$) and sine whistles ($r = .55$) differentiated mouthing from bite/rake, and on function two, constant whistles ($r = .88$) differentiated bite/rake from open mouth.

Univariate Analyses of Variance (ANOVA) and Post Hoc Tests

The MANOVA was followed up with univariate ANOVAs. There was a significant relationship in the rate of constant whistles across behavior type, F

$_{(2,674)}=11.23$, $p < .05$, in the rate of convex whistles across behavior type, F $_{(2,674)}=11.24$, p < .05, in the rate of concave whistles across behavior type, F $_{(2,674)}=3.88$, $p < .05$, and in the rate of sine whistles across behavior type, F $_{(2,674)}=8.30$, p < .05. The post hoc analysis using Tukey's HSD revealed that upsweep whistles were the only whistle shape not to significantly differ in rate based on behavior type. There were more constant whistles (Figure 11a) during bite/rake compared to open mouth (p=.000); more downsweep (Figure 11b) whistles during open mouth compared to mouthing (p=.000) and more downsweep whistles during open mouth compared to bite/rake (p=.000); more convex (Figure 11c) whistles during mouthing compared to open mouth (p=.000) and more convex whistles during mouthing compared to bite/rake (p =.001); more concave (Figure 11d) whistles during mouthing compared to open mouth (p =.022) and more concave whistles during mouthing compared to bite/rake (p =.039); and more sine whistles (Figure 11e) during mouthing compared to open mouth (p =.000) and more sine whistles during mouthing compared to bite/rake (p=.001).

a.

b.

c.

d.

e.
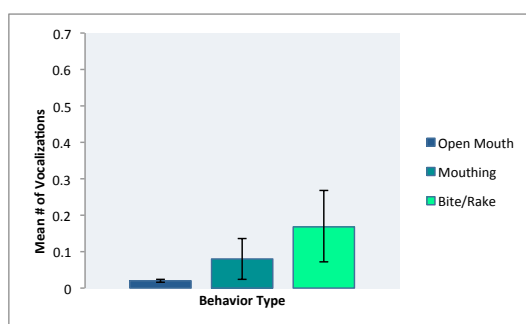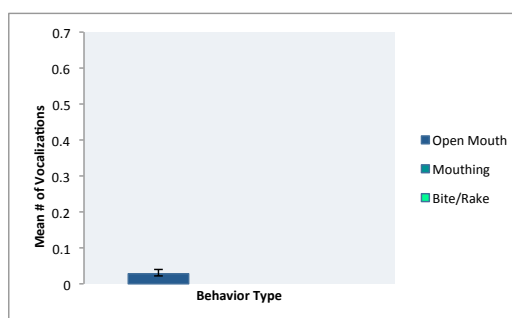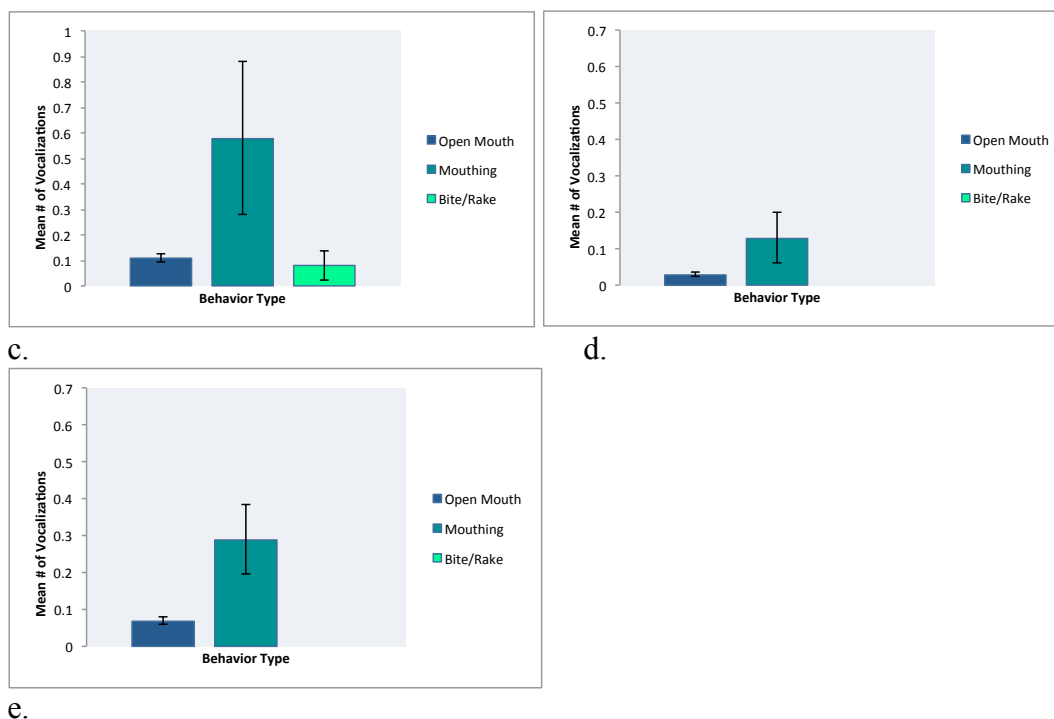
Figure 11. Significant Differences, Illustrated in Post-Hoc Comparisons, in the Average Number of Constant Whistles Across Behavior Type (A), Downsweep Whistles Across Behavior Type (B), Convex Whistles Across Behavior Type (C), Concave Whistles Across Behavior Type (D), and Sine Whistles Across Behavior Type (E).

Whistle Contour and Social Context

Multivariate Analysis of Variance (MANOVA)

Using Pillai's trace, there was a significant relationship between social context and whistle contour rate, V=0.08, $F_{(36, 4020)} = 1.56$, $p < .05$.

Discriminant Analysis (DA)

The MANOVA was followed up with a discriminant analysis, which yielded six discriminant functions. Function one had canonical $R^2 = .05$, and all functions together significantly differentiated the contexts, $\Lambda = .92$, $\chi^2(36) = 56.45$, $p=.016$. On function one, sine whistles ($r = .60$) and upsweep whistles ($r = .53$) differentiated non-aggressive social from herding contexts.

Univariate Analyses of Variance (ANOVA) and Post Hoc Tests

The MANOVA was followed up with univariate ANOVAs. There was a significant relationship in the rate of upsweep whistles across social context, $F_{(6,670)}=2.30$, $p < .05$, and in the rate of sine whistles across social context, $F_{(6,670)}=2.13$, $p < .05$). The post-hoc analysis using Tukey's SDF was not significant for any of the contours and social context. Post-hoc tests are more conservative, and this inconsistency is likely due to the small sample sizes of each contour.

Mouthing Behaviors in Silence

Behaviors coded as silent were those that occurred without the presence of defined vocalization types; therefore, these results might be a conservative estimate. Only 4% of mouthing behaviors of any type occurred in silence (N=26) (Figure 12). Behavioral instances in silence were most often open mouth displays that occurred during either a non-aggressive social context (N=11) or a socio-sexual context (N=9) (Figure 13). All three mouthing behavior types occurred at some point during silence, and herding was the only social context to never occur in silence (Figure 13).
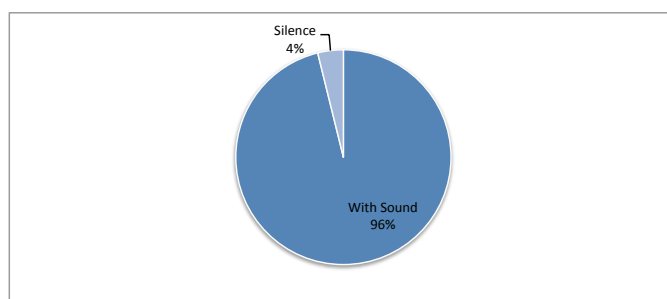
Figure 12. The Percentage of Instances that Occurred With vs. Without Sound.
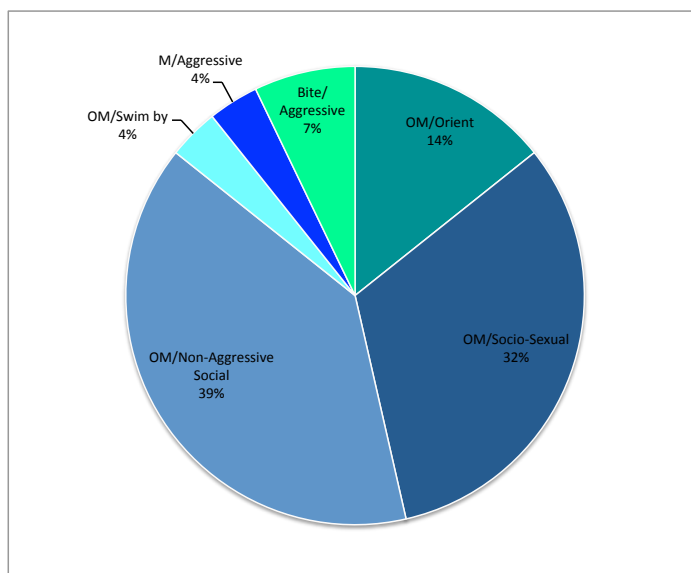
Figure 13. The Percentage of Instances that Occurred in Silence According to the Specific Behavior and Context. M=mouthing, OM=open mouth, Bite=bite/rake

CHAPTER V

DISCUSSION

Previous studies on a variety of cetacean species suggest flexibility in the use of vocalizations during differing behavioral states and contexts. However, we do see patterns emerging in the literature that demonstrate a tendency to use certain types of sounds more or less frequently during certain situations. The results of the current study suggest that dolphins use seven vocalization types differently when behavior type changes and also that social context plays an additional role in determining sound use. While burst-pulse type B and whistle squawks were the most frequent vocalizations during the study period, it is pertinent not only to determine which sounds are most prevalent during all behaviors, but also to examine how each vocalization is used when behavior changes. This behavioral component is an important comparison as all three behavior types in the current study are related.

Vocalizations According to Mouthing Behavior Type

The types of vocalizations that bottlenose dolphins emit during mouthing displays differ based on the specific mouthing behavior exhibited. It is interesting that the highest average vocalization rates are during instances of mouthing (Appendix C). It is possible that this type of display is the most ambiguous, and additional acoustic signaling is therefore needed to efficiently convey information. The influence of social context is discussed later. Additionally, since whistles, chirps, and whistle squawks were significantly more prominent during mouthing than either other behavior type, it is possible that frequency modulated sounds are indicative of amiable interactions in the context of mouthing behaviors. One possible explanation of why biting and raking events

were accompanied by fewer vocalizations overall (Appendix C) may be that the behaviors themselves are meaningful enough without the added acoustic signals. Since echolocation clicks were present in less than half of all behavioral instances, it is unlikely that they play an important role in information exchange during mouthing behaviors. This result is not unexpected, as echolocation signals are traditionally segregated from communication signals (Tyack, 2000; Zimmer, 2011). It is possible that clicks heard during mouthing behaviors were emitted from dolphins not engaging in mouthing behaviors, since the localization of sounds to individuals was not possible within the current data set.

Not all vocalization types differ in rate across behavior types. Dudzinski (1998) concludes that the same sounds are used across different behavioral contexts, suggesting a diverse significance in the use of vocalizations. The current study supports this conclusion, suggesting that certain vocalizations are used differently as mouthing behavior type changes. The difference in the production rate of whistles, whistle-squawks and chirps with respect to behavior type suggests that dolphins primarily use frequency modulation to exchange information with conspecifics during mouthing behaviors. This finding is important, and future studies should utilize a wider variety of frequency-modulated sounds to target how dolphins are using tone across behaviors. In the literature, whistles are heard during social play and aggression (Dudzinski, 1998), during alloparenting and mother calf interactions (Herzing, 1996) and during feeding (Herman & Tavolga, 1980). This study provides data that adds mouthing behaviors overall, and specifically instances of mouthing as whistle were most prominent during this behavior, to the list of behaviors frequently associated with whistles. Whistle squawks are

reportedly heard during aggressive behaviors as well as sexual play (Herzing, 1996), and in this study most prominently during mouthing. The lack of difference in the emission rate of pulsed sounds across behavior type indicates that they are not as important in predicting behavioral state based on sound. In research by Overstrom (1983) in an assessment of burst pulse sounds during aggression, only pulsed sounds were heard during open mouth displays, while the current study documents all seven vocalization types present during open mouth displays. This finding illustrates the limited research on mouthing behaviors and indicates that we can only begin to understand how sound is used during these behaviors through continued research.

<center>The Role of Social Context</center>

It is important to first note that due to small individual sample sizes for the interaction, all three types of mouthing behaviors were grouped together for the analysis across social contexts. Therefore, specific conclusions regarding individual types of behavior during differing contexts for the current data set are not available. Mouthing behaviors occurring during aggressive contexts are loudest, and whistle squawks specifically had the highest average vocalization rate. In the literature, aggressive contexts tend to invoke the need for louder or more intense acoustic signals, as there is a lot of information to share and gain in these settings (Tyack & Clark, 2000). The current study demonstrates the use of both tonal and pulsed sounds during aggression, suggesting the need for both sound types in this context. Certain vocalization types are absent during certain contexts, indicating the use of specific vocalizations to convey different information depending on the context. Whistle squawks and burst-pulse type B vocalizations are consistently more common during aggressive contexts than any other.

In the literature, aggressive contexts are characterized by a variety of sounds, including whistles, squawks, whines (Dudzinski, 1998; Herzing, 1996), and burst-pulse sounds (Blomqvist & Amundin, 2004). The presence of both frequency-modulated and pulsed sounds during mouthing behaviors in an aggressive context reflects this previous documentation of a variety of sound types used during aggression. Conversely, whistles and burst-pulse type A vocalizations are more common during non-aggressive social contexts compared to aggressive contexts. Similarly to aggressive contexts, both tonal and pulsed sounds are used, but whistles are slightly more common (Appendix D). Thus, frequency modulation seems to be more important in non-aggressive settings compared to aggressive settings. Given that whistles are also more common during instances of mouthing, it is probable that whistles in the context of mouthing behaviors indicate amiable interactions. Overall, the level of aggression is important in assessing information exchange during mouthing behaviors. One important note is that it is possible that the social context labeled "non-aggressive social" may have pooled too many categories together. In the future, this category should be carefully separated into more precise contexts.

While moans did not differ significantly in rate across either behavior type or social context, they were consistently not significant. It is likely that moans are not used in information exchange during mouthing behaviors. In the literature, moans are infrequently noted (dos Santos et al., 1990), and they are noted in advance of interactions with humans or trainers (van der Woude, 2009). The moans heard during mouthing behaviors may be a result of the videographer in the water or may be from dolphins not actively engaging in mouthing behaviors. Social context influences the use of only

certain vocalization types, indicating that for pulsed sounds, social environment is more important than behavior type in understanding vocal usage during mouthing behaviors. Overall, one can conclude that it is not sufficient to examine only behavior type when assessing vocalizations as a part of information exchange.

<div align="center">Variations in Whistle Contour</div>

In the literature, whistles are classified based on their contours (Janik, 1999). In the current study, upsweeps are the most common whistle contour of bottlenose dolphins, followed by convex and sine whistles. Interestingly, this finding is similar to that in Bazúa-Durán and Au (2002) who found upsweep, sine, and convex whistles, respectively, to account for the majority of whistles produced by Hawaiian spinner dolphins. All whistle contours, with the exception of upsweeps that are consistently common across behaviors, vary significantly in rate across behavior type. It is possible that some of the whistles emitted during mouthing behaviors are signature whistles, which show the same contours throughout repetitions (Caldwell & Caldwell, 1965). Dolphins distinguish conspecifics by different whistle contours (Janik, Sayigh, & Wells, 2006). Thus, dolphins may use whistles to identity each other during mouthing behaviors. To the author's knowledge, there is no published research on the signature whistles of the dolphins at RIMS. The lack of difference between whistle contour and social context indicates that the use of whistle contours by dolphins across mouthing behaviors is more important than varying contour across social context. According to the literature, no previous relationships between whistle contour and social context have been documented (Janik, 2009).

Behaviors in Silence

While all three behavior types are noted in silence, these behaviors are not a substantial portion of the data set and there is no pattern to when behaviors occur in silence. As such, the current data suggest that mouthing behaviors are more significantly associated with sound, and one can conclude that sound is an important part of exchanging information in the framework of mouthing behaviors. In the literature, social behaviors are frequently discussed in relation to accompanying vocalizations, and mouthing behaviors are often social in nature. In the current data, mouthing behaviors in a herding context are always accompanied by sound. Herding is previously associated with male alliances interacting with females (Connor, Smolker, & Richards, 1992), and research has suggested that herding involves a vocal element termed a pop (Connor & Smolker, 1996). Still, it is possible that mouthing behaviors within a herding context do occur in silence, and a larger dataset allowing for an interaction analysis of specific behavior type according to each context would allow for a more detailed assessment.

Study Implications

Mouthing behaviors are characterized by a variety of sounds that differ in production rate across both behavior types and social contexts. More importantly, for certain vocalizations, rates only differ across certain behaviors or certain contexts. This difference suggests that there is some level of structure to information exchange during mouthing behaviors in dolphins. Bottlenose dolphins have a repertoire of numerous vocalizations (Tyack & Clark, 2000), yet different vocalization types are more prevalent during certain behavior types than others. Moreover, these differences are statistically significant. As such, there are likely many factors that influence the type of vocalization

emitted within specific behavioral contexts. Because the possible factors affecting information exchange during mouthing behaviors are unknown, continued research is needed.

Current literature on mouthing behaviors is limited. The current study is the first to document a sound-behavior parallel during mouthing behaviors. However, the final interpretation of vocalizations during mouthing behaviors likely depends on the behavioral context leading up to the actual mouthing event, as the mouthing behavior could be a direct response to prior interactions. Additionally, the context of behaviors directly succeeding the mouthing event should be considered, as they may be a product of the mouthing behavior. Accordingly, vocalizations in the time frame surrounding each mouthing event must be analyzed to make more succinct conclusions regarding the function of vocalizations. Regardless, the data from this study indicate that it is pertinent to examine mouthing behaviors as separate behaviors, rather than a single category of behaviors, in order to understand differences in how and what information is exchanged. Once these behaviors are better understood, researchers can analyze the context of individual instances of mouthing behaviors and the associated vocalizations of known individuals. These results could lead to more specific conclusions regarding how conspecifics exchange information during mouthing behaviors, which are behaviors not limited to dolphins (see also dogs (Godbout & Frank, 2011), human infants (Rochat, 1989), and rats (Smotherman, Arnold, & Robinson, 1993)).

APPENDIX A

MOUTHING DISPLAY DEFINITIONS

| Mouthing Display	Definition
Open Mouth Display (OM)	Dolphin opens mouth, often exposing teeth, in orientation to another conspecific
Bite/Rake (Bite)	Dolphin closes mouth with force around another dolphin on any part of the body (bite), or rubs/slides it's jaw, with teeth, along a conspecific (rake)
Mouthing (M)	Dolphin has mouth around conspecific's body, but is not biting down

Note: Definitions adapted from Seay et al., (2011)

APPENDIX B

MOUTHING CONTEXT DEFINITIONS

| Mouthing Context	Definition
Aggressive	Displays frequently include abrupt vertical head movements and/or chasing
Herding	Displays occurring in a pair swim when one individual displays ahead or slightly to the side the second individual is on
Orient	Displays occurring when both are in the vicinity and one orients to another but it is not social, aggressive, or social-sexual in nature
Socio-sexual	Displays occurring during attempted mounting or copulation -General: Not directed at another, typically occurs when individual has been mounted -Specific: Directed display at another
Non-aggressive social	Displays that includes side or ventral to surface body orientation, and possibly melon bumping and/or rubbing. No behaviors from other social contexts are present
Swim by	Displays as individuals pass by each other, and neither stops nor stays in vicinity

Note: Definitions adapted from Seay et al., (2011)

APPENDIX C

AVERAGE NUMBER OF VOCALIZATIONS BY TYPE ACCORDING TO

BEHAVIOR TYPE
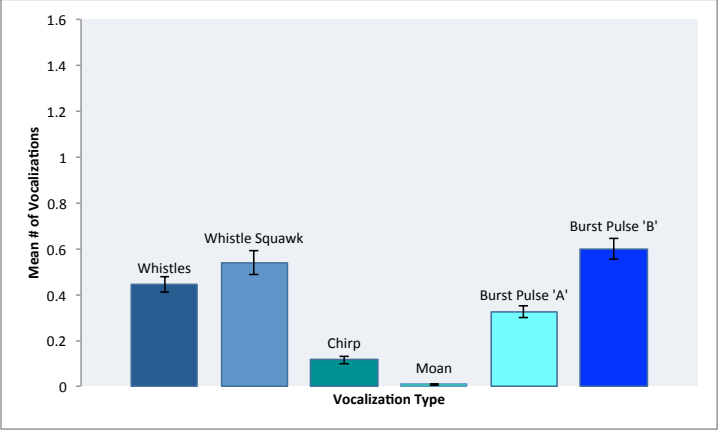
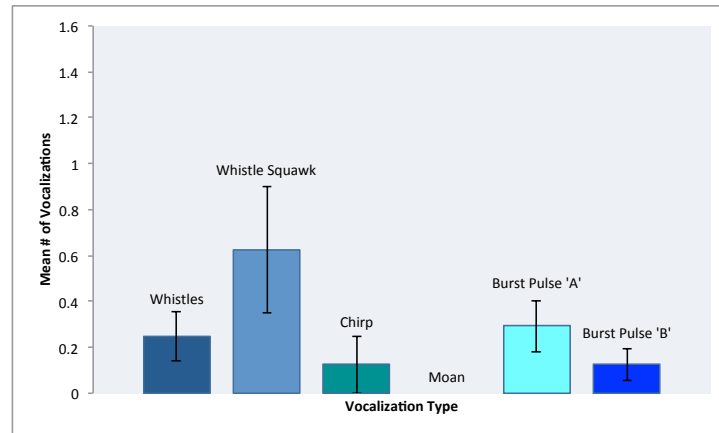a. Average number of vocalizations by type during open mouth displays.
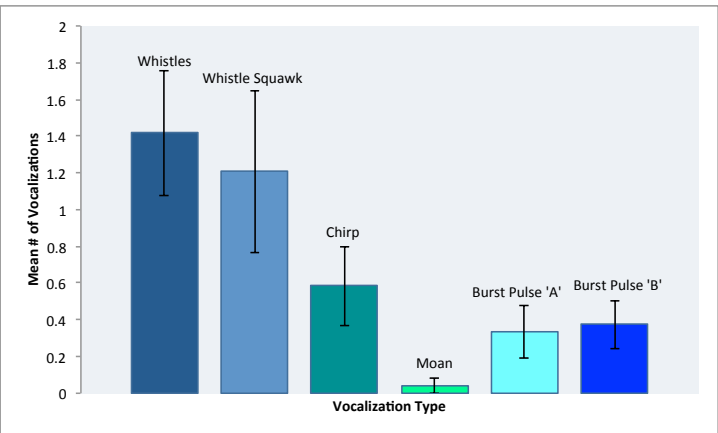
b. Average number of vocalizations by type during mouthing.

c. Average number of vocalizations by type during biting/raking.

APPENDIX D

AVERAGE NUMBER OF VOCALIZATIONS BY TYPE ACCORDING TO SOCIAL
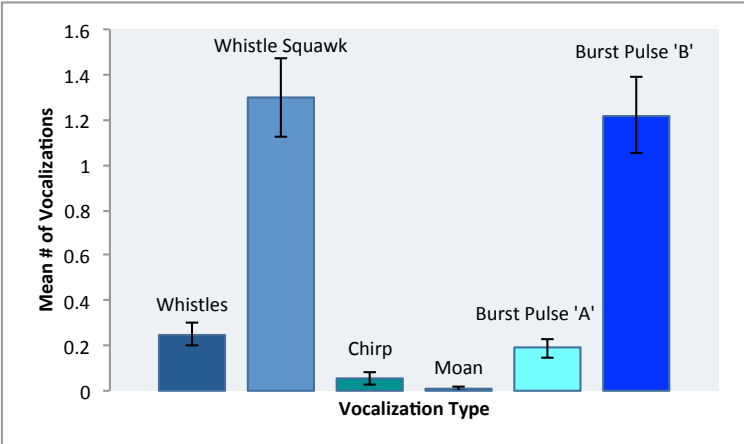
CONTEXT

a. Average number of vocalizations by type during aggressive contexts.
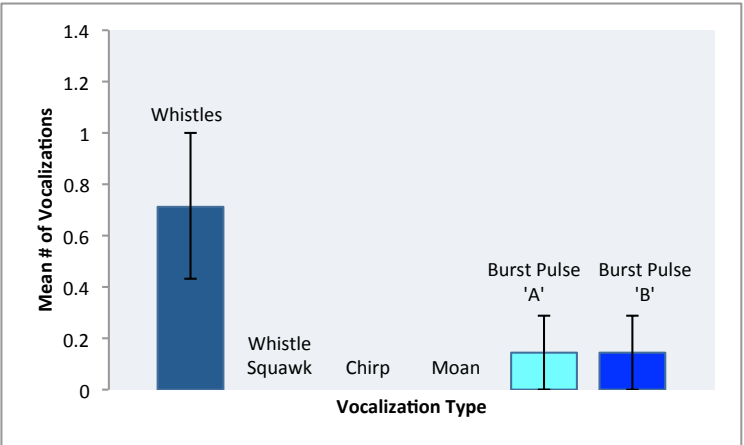
b. Average number of vocalizations by type during herding contexts.
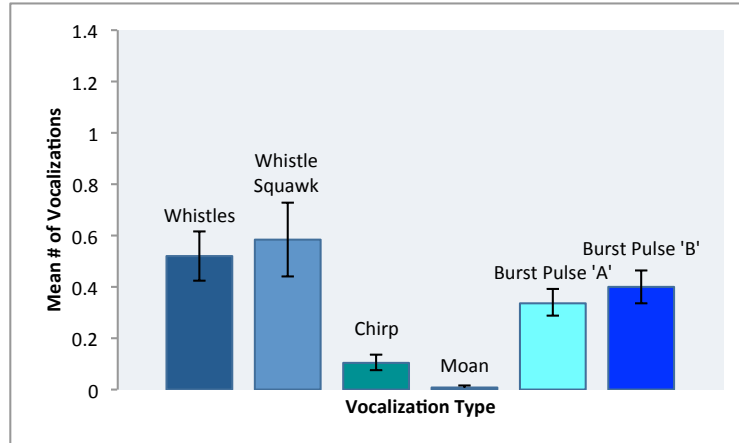
c. Average number of vocalizations by type during orienting contexts.

d. Average number of vocalizations by type during socio-sexual contexts.
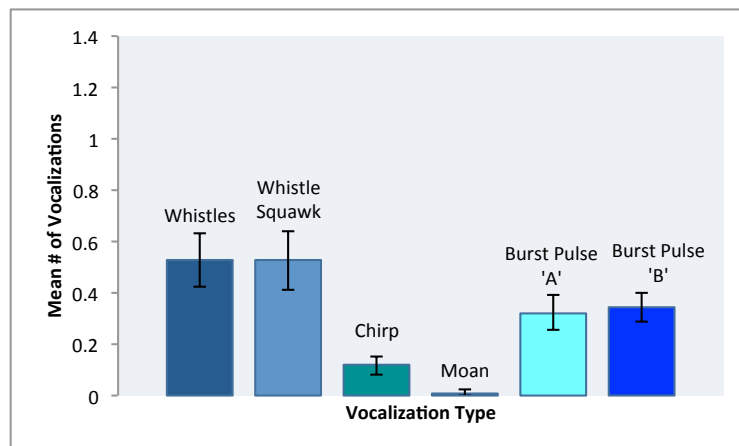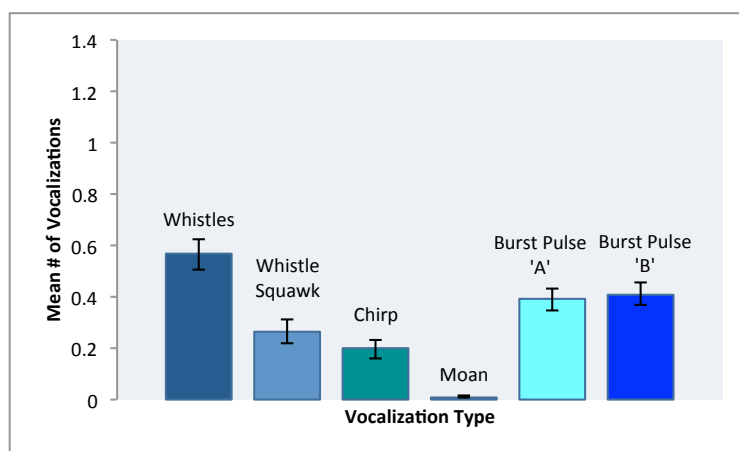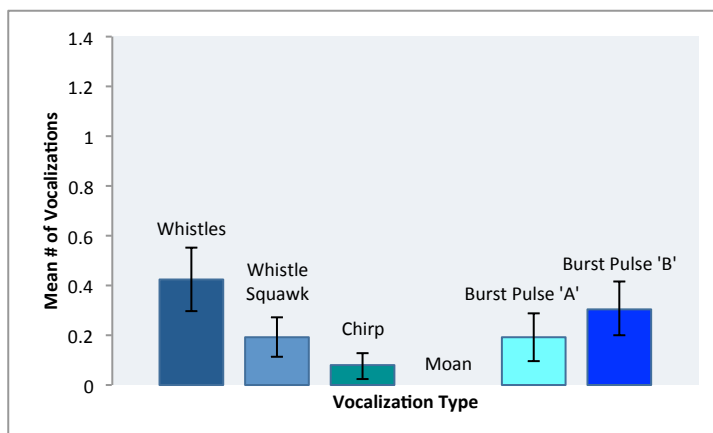

e. Average number of vocalizations by type during non-aggressive social contexts.

f. Average number of vocalizations by type during swim by contexts.

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