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A review of bottlenose dolphin (*Tursiops truncatus*) vocalizations and an investigation into the existence of signature whistles in a captive dolphin population

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Table of Contents

Abstract

Individual recognition of conspecifics is important for various reasons in both terrestrial and marine dwelling species and is carried out through a variety of modes including visual, chemical and auditory cues. The ability to recognize individuals acoustically is often carried out through the use of signature vocalizations. The production and use of signature whistles within bottlenose dolphins has been extensively tested since their existence was first suggested almost 50 years ago. From the research, two primary hypotheses have emerged: the signature whistle hypothesis and the whistle repertoire hypothesis. This work discusses the various acoustical means of individual recognition found within the animal kingdom and narrows to discuss bottlenose dolphin communication and the evidence supporting these two existing hypotheses. The results from a previously unanalyzed data set, presented within this work, support the existence of individually distinct whistle contours in captive bottlenose dolphins as well as the concept that shared whistle contours, like the upsweep style whistles, probably play an important role in communication.

Keywords: Animal communication; Individual identification; Signature whistles; *Tursiops truncatus*

Literature Review and Synthesis

Introduction

Recognition of distinct individuals can be important for many reasons in nature. For example, kin recognition is a form of individual identification that aids in the avoidance of inbreeding (Cassinello & Calabuig, 2008; Nelson-Flower et al., 2012), the avoidance of cheaters in cooperative societies (Ho et al., 2013), and may lead to preferential treatment of related individuals (Ceacero et al., 2007). Several studies have been conducted on herd dwelling animals that suggest evidence of mothers being more responsive to signals from their own offspring rather than other similarly aged calves (Marchant-Forde et al., 2002; Terrazas et al., 2003; Torriani et al., 2006). The ability to recognize their own offspring in a large group is also important to colonial pinniped mothers (Charrier et al., 2010; Pitcher et al., 2012; Van Opzeeland & Van Parijs, 2004). Being able to recognize and select ideal mates is an important biological function that can help prevent genetic incompatibility (Lindholm et al., 2013; Thiel et al., 2013).

Individual recognition can be accomplished by a variety of modes within the animal kingdom. Chemical cues in the form of pheromones can aid in the location of mates (Passos et al., 2013), and individually distinct pheromones called "signature mixtures" may allow for individual recognition (Wyatt, 2010). Facial variations may be useful to monochromatic animals as visual cues for recognizing individuals (Kondo & Izawa, 2014). Acoustic cues aid in the identification of individuals through the use of signature vocalizations which are individually distinct communication signals. (Shapiro, 2010). Sound cues may be particularly useful in marine environments as sound travels more efficiently through water than air and, as such, can be a useful means of communication for marine animals, especially cetaceans.

Bottlenose dolphins (*Tursiops truncatus*) are distributed globally in both coastal and pelagic water. Their common occurrence in captivity has enabled numerous studies on their sound production and reception capabilities (Harley, 2008). Bottlenose dolphins, like most delphinids, produce both echolocation clicks and narrowband whistles. Clicks are used primarily to identify objects (Harley et al., 2003), while whistles are used for communication (May-Collado & Wartzok, 2008). "Signature whistles" in bottlenose dolphins were first proposed by Caldwell and Caldwell (1965), and have since created a topic of intense debate as to which types of whistles carry information about the vocalizing individual to conspecifics. There are two predominant hypotheses relating to this topic: the signature whistle hypothesis, suggests that individually distinct or "signature whistles" in bottlenose dolphins are used to carry information about the identity of the vocalizing individual to surrounding conspecifics while the opposing whistle repertoire hypothesis, suggests that bottlenose dolphins produce primarily whistles from a whistle repertoire that is shared amongst not only dolphins that are familiar with one another but also dolphins from different geographical populations and that the variations in the whistle characteristics of these shared whistle contours, carry identity information about the vocalizing individual. This capstone is set within the broader conceptual framework of recognition through the use of signature vocalizations in non-human conspecifics and will narrow to address the following objectives:

1. Summarize current knowledge of bottlenose dolphin vocalizations.
2. Summarize research related to the two predominant signature vocalization hypotheses in bottlenose dolphins
3. Present a previously unanalyzed data set that provides insight into the existence of signature whistles in free-swimming, captive bottlenose dolphins.

Signature Vocalizations

Vocal communication for the purpose of individual recognition is important in many species (Shapiro, 2010). Perhaps the most compelling evidence for the existence of signature vocalizations can be found in mother-calf pair experiments. Studies conducted on terrestrial herd animals provide excellent examples for the use of these types of vocalizations. Newborn dairy calves show behavioral responses to sound playbacks of their own mother's call even after being removed from their mothers within the first 24 hours of life (Marchant-Forde et al., 2002). Calf responses to their own mother's call included increased heart rate, head/ear twitching, and orientation towards the speaker (Marchant-Forde et al., 2002). Evidence of interindividual variability in newborn goat vocalizations and the overall orientation towards the sound source of their own offspring's calls suggest that mother goats may be able to use vocal cues to aid in the identification and location of their own offspring (Terrazas et al., 2003). Fallow deer (*Dama dama*) display a unidirectional identification method where mothers produce individualized vocalizations, but there is little or no perceived individuality within calf vocalizations (Torriani et al., 2006). The use of signature vocal cues is not limited to the terrestrial environment. Marine organisms use vocal cues as a means of individual identification as well, particularly marine mammal species. Colonial pinnipeds often give birth and raise their pups in chaotic, highly populated environments (Halliday, 1990). Mothers leave their offspring on the beach in order to forage but face the task of re-locating their pup on the sometimes densely packed beaches. Atlantic walrus *(Odobenus rosmarus)* mothers have been observed to be more responsive to the barks of their own pup indicating that vocal calls play a key role in mother-pup reunions (Charrier et al., 2010). Australian sea lion (*Neophoca cinerea)* females use a combination of temporal, amplitude and frequency parameters in their offspring's vocalizations to differentiate their call from the calls of similarly aged pups (Pitcher et al., 2012). In some species, it is important for mother-calf recognition cues to be formed quickly. Harp seals (*Pagophilus groenlanduicus)*, for example, have a lactation period of only 11 days with vocal cues for mother-pup reunions become unnecessary after that time period. Even in this short-term bonded species, evidence suggests that acoustic signals, along with visual and olfactory cues, play a role in mother-pup reunions on ice floats (Van Opzeeland & Van Parijs, 2004). Vocal recognition can be important on a larger scale as well. In social species, populations are often subdivided by researchers into smaller units of individuals that appear to live in communities (primates) or clans (cetaceans) (Kappeler & van Schaik, 2002; Matkin et al., 2014). It has been suggested that different killer whale (*Orcinus orca)* clans in the Northern Pacific may use the same set of stereotyped whistles in order to maintain connections with members of other clans (Riesch et al., 2006). Because killer whales live in rigid matriarchal structures, it is likely that group dialects play a more important role than recognition on an individual level within this particular species (Riesch et al., 2006). Bottlenose dolphins, on the other hand, live in fission-fusion societies with some relationships being more rigid and longer lasting than others (Mann et al., 2000; Reiss et al., 1997). In a society where certain individuals maintain long-term bonds while associating with others in a more casual way, signature whistles likely play a more important role in individual recognition.

Dolphin Acoustics

Dolphins are capable of creating a variety of vocalizations from narrowband whistles to high frequency echolocation clicks. Most odontocetes use echolocation to locate and identify objects (Harley et al., 2003) and frequency-modulated tones (whistles) for con-specific communication (May-Collado & Wartzok, 2008). A few species, like the Hector's dolphin (*Cephalorhynchous hectori),* may also use clicks for communication as their vocal repertoires do not contain whistles. This type of vocal repertoire that uses only clicks may allow dolphins to obtain information from their own vocalizations as well as the clicks of surrounding dolphins when in large groups where the likelihood of vocal masking may be more prominent (Dawson, 1991).

The production of whistles has been studied extensively in several dolphin species with a wide range of vocalization capabilities (Solntseva & Rodionov, 2012). Bottlenose dolphin “whistles” are produced by vibrating tissue in the nasal system and as such the term "whistle" is actually a misnomer (Madsen et al., 2012). Madsen and colleagues (2012) found that the frequency contours of bottlenose dolphins were maintained when produced in either an air or a heliox (mixture of helium and oxygen) setting. Because sound travels faster in a heliox system, the fact that overall whistle contours were maintained suggests that these dolphins produce whistles in a manner that is analogous to the way humans produce speech, by vibrating tissue rather than actually producing whistles. This particular physiological adaptation probably evolved as a way to maintain successful communication despite the frequent changes in hydrostatic pressure that come about while diving.

There is some debate as to when a dolphin's whistle repertoire is developed. Some studies suggest that dolphins develop a basic whistle repertoire that includes an individually distinct signature whistle within the first year of life (Caldwell & Caldwell, 1965; Caldwell et al., 1990). Others suggest that there is no evidence of a persistent individually distinct whistle within that first year (McCowan & Reiss, 1995b). McCowan and Reiss (1995) documented the vocalizations of eight captive born dolphins over the first year of life and found that while 94 of the 128 (73.4%) whistle types were seemingly unique to individual calves (only produced by 1 infant), all but three of those 94 whistle types were also unique to the developmental stage of the calf. The authors suggested that there is a high turnover rate within calf repertoires between developmental stages and individually distinct whistles were not necessarily maintained. Caldwell and Caldwell (1990), on the other hand, studied 14 infant bottlenose dolphins and concluded that all but one of those dolphins developed a stereotyped whistle by the end of their first year. Whether or not these conflicting data are a result of different methodologies remains to be seen and, as such, a debate will remain until further research can provide clarification on the subject.

One thing that most researchers seem to agree on is that learning plays an important role in whistle development. In an experiment conducted on 10 dolphin pairs that consisted of one free-ranging and one captive dolphin matched for age and sex, results indicated that captive-born calves were more likely to produce simpler, less frequency modulated whistles than a free-ranging individual of the same age and sex (Miksis et al., 2002). The authors hypothesized that this may be due to vocal learning that occurs between captive calves and the training whistles used by the humans to whom they are frequently exposed (Miksis et al., 2002). One study of a captive beluga whale (*Delphinapterus leucas*) named NOC suggested that some odontocetes may be capable of mimicking human speech (Ridgway et al., 2012). Another study conducted on captive dolphins suggested that mimicry and exposure to interactive environments may facilitate the learning of functional whistles (Reiss & McCowan, 1993). In this study, Reiss and McCowan exposed two sets of mother dolphins and their male calves to an underwater keyboard that provided certain objects or activities accompanied by specific computer-generated whistles when certain keys were pushed. Over the first year of the study, mimicry of computer-generated whistles was observed. Within the second year, reproductions of these synthetic whistles were used in behaviorally appropriate contexts by the male dolphins. Free-ranging animals also provide evidence of vocal learning. For example, killer whales have been observed to increase the production of their family-specific calls immediately following the birth of a new calf. Whistle production returned to normal within the first two weeks of the calf's life (Weiss et al., 2006). This behavior may facilitate learning by the neonate and decrease the time necessary for a calf to recognize and learn family whistle structure. Evidence collected from free-ranging, adult bottlenose dolphins suggests that male partners in highly stable male-male alliances are more likely to have similar whistles than non-partners (Watwood et al., 2004). The authors suggest that vocal learning may enable male dolphins to develop a signature vocalization that is similar to their partner's, which in turn may help facilitate or may be a direct product of a stronger social relationship. Studies have also shown that male bottlenose dolphin calves are more likely to produce whistles similar to those of their mothers as compared to female calves (Sayigh et al., 1990; Sayigh et al., 1995). This may be a result of the social structure of dolphins as female philopatry has been observed in bottlenose dolphins

(Moller, 2012), and many female-female associations are determined, at least in part, by matrilineal and bipatrental relatedness (Frere et al., 2010). Therefore it has been hypothesized that females produce whistles that are distinct from their mother's whistles in order to allow for easier differentiation of closely related female individuals.

In a review of the signature whistle hypothesis, Caldwell et al. (1990) suggested that whistles develop and change throughout various stages of life. The authors reported that various whistle characteristics changed with increasing age: whistle characteristics like number of loops, duration and frequency modulation were all observed to increase with age suggesting that vocal learning may not stop during the early developmental stages. However, Caldwell et al. (1990) also noted that the overall contour shape of three out of four dolphins they studied long-term were maintained for long periods of time, with the longest duration for whistle signature maintenance at 18 years. The only dolphin whose signature whistle was not maintained lost his signature whistle completely and produced a seemingly unlimited number of other whistle types. Some of the whistles he produced were mimics of playback tones to which he had been exposed while others were multi-loop whistles that were not similar to his own previously used signature whistle nor to the signature whistles of other dolphins. This particular dolphin had been isolated from conspecifics for 7 years during which time he was exposed to many recorded natural and synthetic signature whistles leading the researchers to question if the observations made on this particular dolphin may be indicative of the long-term effects that playback and mimicry experiments can have on the vocal repertoires of dolphins.

Proposed Uses of Whistles

Dolphin whistles are used for communication (Reiss et al., 1997). Communication signals throughout the animal kingdom are often complex and may depend on several different factors including social structure and environmental characteristics (Goodenough et al., 2010). Bottlenose dolphins can alter the fundamental frequency of their whistles when in the presence of high ambient noise levels (May-Collado & Wartzok, 2008); dolphins produced higher frequency whistles with increased frequency modulation when in the presence of multiple boats. In addition to altering the actual characteristics of an animal's vocalizations, environment and social structure may facilitate alterations to communicative behavior. Bottlenose dolphins off the coast of Scotland decreased production of individual whistles when in larger groups (Quick & Janik, 2008). It was suggested that even though these dolphins are prone to produce whistles in social environments, when a group of dolphins gets too large acoustic masking may make production of individual vocalizations ineffective.

Research has provided insight into the different factors that may influence the structure of dolphin communication, and specifically bottlenose dolphin whistles (Markov & Ostrovskaya, 1990). A study conducted on the hierarchical structure of dolphin communication suggests that a dolphin's whistle holds a significant amount of information about the next whistles that will occur in a sequence (Cancho & McCowan, 2012). Nakahara and Miyazaki (2011) identified a temporal pattern between two communicating dolphins. When an individual dolphin responds to the call of another dolphin's signature whistle, the response often occurs less than one second after the original call has ended. In contrast, if there is no response by a second dolphin, the original vocalizer may repeat the original call, usually more than one second after the original call is ended (Nakahara & Miyazaki, 2011).

The proposed uses of specific whistles are varied and cover a range of topics that may be important to communication among conspecifics. One example is in the use of a distress whistle. Caldwell et al. (1990) indicated that certain alterations to the typically stereotyped whistles frequently observed may have been indicative of distress. In several of their studies, temporary restraint or separation from other dolphins was used in order to assure accurate identification of the vocalizing individual. During some trials, the authors observed unusual alterations to the signature vocalizations (Caldwell et al., 1990). Changes in amplitude and duration of the whistles as well as abrupt stops in the whistles were also observed, leading to the suggestion that these changes may convey the distressed status of the individual. Herzing (1996) suggested that a combination of whistles and burst-pulses may be indicative of a distressed or excited state among bottlenose dolphins and Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. A behavior and acoustic study on dolphins in the Mediterranean Sea suggested that certain whistle features (e.g., peak frequency and duration) may provide information about the behavioral state of the animal in varying contexts (Lopez, 2011). It has also been proposed that using these various parameters may be a functional, non-invasive method of detecting the stress level of an animal (Esch et al., 2009). However, further research is necessary to correlate vocalization parameters to physiological stress responses.

The phenomenon of one dolphin copying another dolphin's whistles has also been well documented. Male dolphins in male-male alliances and mother-calf pairs are the most likely individuals to be observed copying their counterpart's signature vocalizations (King et al., 2013). Data suggest that copying another dolphin's whistle may facilitate a stronger social bond between individuals. This hypothesis is further strengthened by evidence that males in male-male alliances use vocal learning to converge upon similar signature whistle contours (Watwood et al., 2004). Playback experiments were conducted with free-ranging dolphins in which signature whistles of certain individuals within the population were played back and resulting vocal responses were recorded (King & Janik, 2013). The study demonstrated that a dolphin responds to the playback of their own signature whistle contour with the production of their signature whistle. These results suggest that perhaps the copying of vocalizations is used to maintain contact between individuals. Finally, a study conducted on captive dolphins has shown that dolphins who are higher in the social hierarchy are more likely to imitate the signature whistles of younger, lower animals than vice versa (Agafonov & Panova, 2012). The data currently available on the topic of mimicry suggests that copying an individual's whistle may play an important role in the maintenance of social structure.

The use of whistles to facilitate mother-calf reunions has also been reported. In a focal study conducted on free-ranging bottlenose dolphins, vocalizations between a young individual (age 0-4) and its mother often resulted in the reunion of the two individuals (Smolker et al., 1993). Usually the calf was observed moving to reunite with his mother but the young dolphin's vocalizations typically incited some kind of response from the mother (Smolker et al., 1993), including the mother vocalizing, slowing or stopping her swimming, or orienting herself towards the young dolphin. In a study conducted on free-ranging bottlenose dolphin mother-calf pairs, both mothers and calves were observed to respond more often to playbacks of their own calf/mother in comparison to their responses towards other similarly aged individuals (Sayigh et al., 1999). Another study conducted on free-ranging dolphins suggests that exchanging whistles may play an important role in the greeting sequence of free-ranging dolphins as they are often observed to vocalize when coming together at sea (Quick & Janik, 2012). Whistles may be used to maintain contact with individuals when they are separated from their group as is common in a fission-fusion society (Smolker et al., 1993). This concept is further supported by a study conducted on free-ranging bottlenose dolphins in Sarasota Bay, Florida, where dolphins were observed to turn more towards whistles emitted from a speaker when those whistles shared the overall contour shape of a related individual (Janik et al., 2006). It would seem obvious that information about the vocalizing individual is being transmitted acoustically; however, there is still some debate as to what types of whistles carry that information and how.

Signature Whistle Hypothesis

The signature whistle hypothesis states that bottlenose dolphins produce individually distinct whistle contours that carry information about the indentity of the vocalizing individual to conspecifics (Caldwell et al., 1990). There have been many studies conducted since Caldwell and Caldwell first identified individually distinct whistles as signature whistles (Harley, 2008; Janik & Sayigh, 2013). Caldwell and Caldwell's original study (Caldwell & Caldwell, 1965), and many subsequent studies conducted by this team were conducted in captive settings. During many of these experiments, accurate identification of the vocalizing individual was conducted by means of forced isolation with the whistles of that isolated individual recorded and converted into spectrograms for visual analysis (See Figure 1 for a spectrogram example). The analysis was completed by human observers who grouped the whistles into categories based on the overall contour pattern (Caldwell & Caldwell, 1965). After several decades of research the authors concluded that certain individuals tend to produce the same unique whistle contour repeatedly (Caldwell et al., 1990).

Whistle Repertoire Hypothesis

While much research to date supports the signature whistle hypothesis (Caldwell & Caldwell, 1965; Caldwell et al., 1990; de Figueiredo & Simao, 2009; Janik et al., 2006; Sayigh et al., 2007; Smolker et al., 1993; Watwood et al., 2005), some studies have presented results for an alternative theory as to how individual identity might be transmitted acoustically to conspecifics. Evidence contradicting the signature whistle hypothesis comes, in part, from the McCowan and Reiss (1995a) study conducted on captive bottlenose dolphins. Instead of forced isolation, the authors used the presence of bubble streams to identify which dolphin was vocalizing while the dolphins were swimming in a group. Another methodological difference between this and the Caldwells' studies relates to how the whistles were categorized. McCowan and Reiss opted for a quantitative method of categorization (McCowan, 1995), rather than using humans to categorize based on overall contour pattern. Their results led to the hypothesis that dolphins have a much more diverse repertoire than the signature whistle hypothesis suggested. The repertoire is shared among dolphins that are familiar with each other, and also with dolphins from different populations (McCowan & Reiss, 1995a). The primary whistle contour observed in the McCowan and Reiss study was a relatively simple upsweep/rise style in which they suggest the variations in characteristics hold the identity information of the vocalizing individual.

Original Research

Introduction

The ability to accurately identify a vocalizer among free-swimming individuals without the aid of visual cues (e.g., bubble streams) can be accomplished with a mobile video acoustic (MVA) system (Dudzinski et al., 1995). For the original research portion of my capstone, I analyzed previously recorded whistle data from free-swimming, captive bottlenose dolphins for visual contour production patterns as a function of vocalizer identity.

Methods

Data Recording

All data included and analyzed for this study were collected from a captive bottlenose dolphin group during two research trips – January 5-14, 2007 and November 2-7, 2010 – by the Dolphin Communication Project (DCP). This captive dolphin group resides at Dolphin Encounters at Blue Lagoon Island, Nassau, The Bahamas. Each underwater observation session was roughly 20-40 minutes in duration. Simultaneous video-acoustic recordings were collected during 1-4 sessions per day using a mobile video/acoustic system (MVA) (Dudzinski et al., 1995). DCP's MVA4 included a Sony HDR-HC1 video camera and two custom-made hydrophones spaced at a minimum distance of 65 cm to account for the difference in underwater sound velocity as compared to our ability to localize to a sound source in air. This design enables researchers to determine audio directionality to a sound source from videotape data (Dudzinski et al., 1995). Video was collected in standard format (2007) and HD (2010). The camera audio sample rate was 32 kHz while hydrophone bandwidth was roughly 150 kHz.

Vocalizer Identification

With simultaneous stereo audio on all videotapes, roughly 38% of all recordings yield the capability to identify the individual vocalizing dolphin(s) (Dudzinski et al., 1995). Confirmations of individual vocalizing dolphin identification(s) were conducted using the left-right-center sound directionality capabilities that are enabled by the MVA design. Distinct individual body scars facilitated correct dolphin identifications from the video footage. Information about age, gender, body position and associates of the vocalizing dolphin were also documented. Dolphin ages were classified using an accepted age/length correlation (Kogi et al., 2004; K.M. Dudzinski, personal communication, 2013). Ages are categorized as: calves are 0-3 years and less than half the length of an adult; juveniles are 3-7 years old and more than half the length of an adult; sub-adults are 7-12 years and between ¾ and full adult length; and adults are 12+ years and about 2 m long. Since this study was conducted in a captive setting, birth dates were known for all dolphins born at the facility. Dolphin gender was known for each study individual. General body position of each vocalizing dolphin was recorded using DCP's ethogram to characterize dolphin body position relative to the water surface. Finally, a vocalizing dolphin was considered to have an associate if another dolphin was also on screen.

Sound Digitizing and Measurements

Audio clips were digitized from videotapes using Raven Pro 1.4, a Sony GV-D1000 NTSC digital cassette player and an iMic sound digitizing computer interface (Griffin Technology). Audio clips were digitized in roughly 10-20 second segments that included at least one whistle. Raven-Pro 1.4 was used to analyze all whistle spectrograms. Measurements included: start/end time of whistle, low/high frequency, 90% bandwidth, 90% duration, 95% frequency, Inter-quartile Range (IQR) bandwidth, IQR duration, maximum frequency, beginning/ending frequencies, signal duration, number of inflections, number of harmonics and octave range.

Whistle Classification System

From videotapes, 2,758 and 1,264 whistles were documented and examined for 2007 and 2010, respectively. For 941 whistles (515 in 2007 and 426 in 2010), the identification of the vocalizing dolphin was confirmed and a JPEG image was created for each of these whistle spectrograms (Figure 1). For the purpose of this experiment, a whistle was considered to be independent and distinct from other whistles if there was a visual break in the whistle. Whistle spectrograms were created with a Hann window, 50% overlap and a 512 FFT.

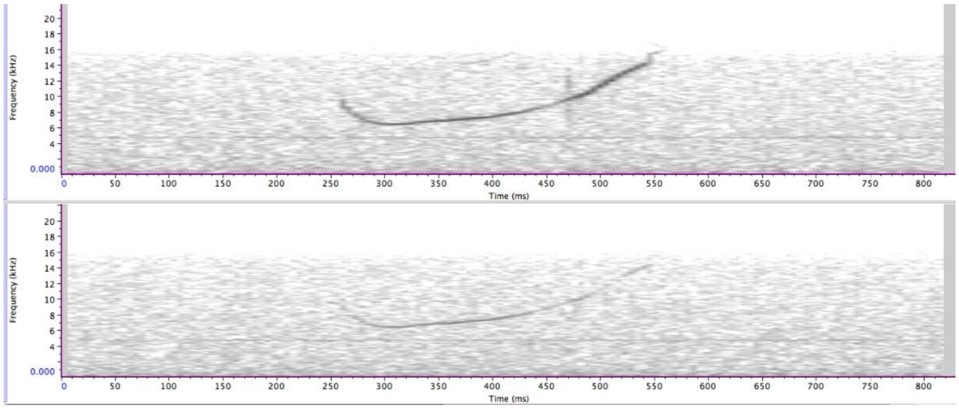


Figure 1: Example of whistle image created for each of 941 whistles that were confirmed to a specific vocalizing dolphin. Each image represented both channels of data (top view/left channel and bottom view/right channel).

Whistles were categorized based on their spectrographic images, which are broadly represented by line drawings (Figure 2). The resulting classification yielded 10 different categories (A-J) and two sub-categories (Fa/Fb) based on general patterns observed from documented whistles. All 941 whistles were placed into their best-fit category by visual inspection. Inter-observer reliability of categories was examined between the author and three separate collaborators (one familiar with and two naive to dolphin whistle production) who classified all 941 whistle spectrograms into the category they felt most accurately represented each whistle contour.

Statistics

The inter-observer reliability of the whistle categorization system created for this study (Figure 2) was examined by calculating the overall proportions of agreement with the author's original classification for 2007 and 2010. The data were examined using chi-square analysis in R, statistical software. Both an asymptotic Chi-square distribution and a Monte Carlo simulation were used to determine the p-values for both the 2007 and 2010 data. A standardized residual test was also conducted in R in order to determine patterns of production for the various whistle contours in relation to individual dolphins, gender or age groups. In order to test for patterns based on individual, gender, and age Chi-square and standardized residuals were run for dolphins whose total number of digitized whistles were greater than 10 (the number of categories in the whistle classification system created for this study).

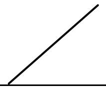
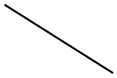
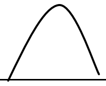
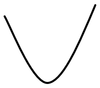
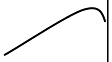
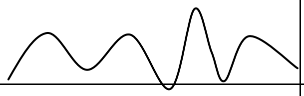
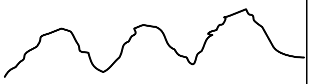
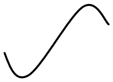
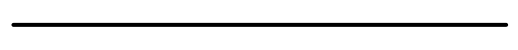
Contour Category	**Shape**	**Description**
A		Whistles are simple, without inflection and increasing slope. Degree of slope and duration may vary.
B		Whistles are simple, without inflection and decreasing slope. Degree of slope and duration may vary.
C		Whistles are convex in shape (upside down U)
D		Whistles are concave in shape (U-shaped).
E	 Or 	The majority of the whistle contour either increases or decreases in frequency and has a single inflection point.
F (type a)		Whistles are multi-loop with ≥2 inflection points. The number of infection points can be highly variable.
F (type b)		Whistles are multi-loop with ≥2 inflection points. The number of infection points can be highly variable. These whistle contours appear "jagged" or stepped.
G		Whistles are "clipped" whistles. These have ≥1 inflection or are multi-loop whistles but the high frequencies are clipped resulting in a one or more of the high-frequency loops being "flattened".
H		Whistles resemble sine waves and have 2 inflection points.
I		Whistles are relatively flat with little to no slope and zero inflections.
J	"Other"	Whistles you feel do not fit into any of the above categories. If you categorize a whistle as "other" please explain why in the comments.

Figure 2: Whistle classification system as created by analyzing whistles attributable to specific/identifiable dolphins from 2007 and 2010 data sets.

Results

Summary of Study Subjects and Whistle Parameters

Tables 1 and 2 summarize several whistle parameters for the dolphins involved in this study for the years 2007 and 2010, respectively. A total of 2,758 whistles were digitized from the 2007 videotapes with 515 of those whistles attributable to a single, identifiable dolphin. From the 2010 videotapes, a total of 1,264 whistles were digitized with 426 of them attributable to a single dolphin.

In total, whistles were attributed to 16 different dolphins over both years. Of these 16 dolphins, four had whistles documented in both 2007 and 2010. There was a wide range in the total number of whistles recorded for each individual over both years ranging from 1 whistle (Gussie Mae and Chippy) to 360 total whistles (Stormy). This study group consisted of 8 male and 8 female dolphins with ages covering all 4 age groups discussed in the methods. Eleven of the dolphins were born at the facility while the remaining 5 were free-ranging caught.

Table 1: Summary of whistle parameters for 2007 by individual

Dolphin ID	**Andy**	**Aunty V**	**Cacique**	**Chippy**	**Miss Merlin**	**Nina**	**Salvador**	**Soca**	**Stormy**
Age	A	A	C	A	S	A	C	S	A
Sex	M	F	M	F	F	F	M	F	M
No. of Whistles	57	9	3	1	32	10	142	107	154
% WHS with bubble stream	1%	11%	0%	0%	38%	60%	0%	17%	12%
% WHS with Associate	1%	0%	0%	0%	16%	100%	0%	0%	0%
Average Min. Frequency (Hz)	5580.7	5473.88	4456.93	5563.1	5996.01	6073.32	5142.26	6022.13	5525.43
Average Max. Frequency (Hz)	12626.12	15289.06	8092.9	14362.8	10270.64	10276.41	12430.78	13435.3	15563.43
Min. Frequency (Hz)	4297.9	4855	2814.9	5563.1	3753.2	4979	4456.9	3691.6	2288.9
Max. Frequency (Hz)	15435.12	16263.1	9734.8	14362.8	15951.1	13022.1	17034.7	16790.4	17472.1
Average Duration (s)	0.62	0.69	0.26	0.618	0.51	1	0.41	0.26	0.18
Average # of Inflections	2.84	5.3	0	5	1.47	6.18	0.67	0.62	0.49
Average # of Harmonics	0.8	0.56	1.33	0	0.53	0.91	0.95	0.66	1.2
Average Octave Range	2.29	2.8	1.92	2.58	1.76	1.7	2.44	2.25	2.96

Table 2: Summary of whistle parameters for 2010 by individual

Dolphin ID	**Andy**	**Clifton**	**Dot**	**Goombay**	**Gussie Mae**	**Jake**	**Laguna**	**Salvador**	**Shawn**	**Soca**	**Stormy**
Age	A	C	A	S	J	A	J	J	A	S	A
Sex	M	M	F	M	F	M	F	M	M	F	M
No. of Whistles	8	22	9	78	1	21	13	29	38	1	206
% WHS with bubble stream	0%	0%	0%	26%	0%	0%	23%	0%	0%	0%	0%
% WHS with Associate	38%	0%	11%	5%	0%	0%	0%	0%	0%	0%	0%
Average Min. Frequency (Hz)	6766.4	6727.24	4784	5826.5	5797.6	5334.7	6075.4	4958.75	6162.2	4976	5288.17
Average Max. Frequency (Hz)	14278	16317.1	14919	16841.14	16727.6	15479	15067.9	14240.7	15125.6	9524	17767.72
Min. Frequency (Hz)	3785.4	5867.4	2059	3823.2	5797.6	2756.2	4181.9	4061.8	4089.9	4976	2090.9
Max. Frequency (Hz)	16467	19198.7	17055	20627.4	16727.6	16538	16252.4	18858.6	20419.8	9524	20705.5
Average Duration (s)	0.52	0.45	0.65	0.36	0.42	0.3	0.674	0.36	0.35	0.15	0.17
Average # of Inflections	1.75	1	4.44	0.17	0	0.48	0	0.97	0.37	0	0.61
Average # of Harmonics	0.75	0.91	0.78	0.52	1	0.9	0	1	0.66	0	1.13
Average Octave Range	2.39	2.44	3.61	2.97	2.89	3.03	2.55	2.89	2.49	1.91	3.69

Inter-Observer Reliability

Tables 3 and 4 summarize my original classifications for each of the whistles in both 2007 and 2010, respectively.

Table 3: Author's Classification for 2007 Whistles

Dolphin	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**G**	**H**	**I**	**J**	**Total**
Andy	14	0	0	2	3	0	37	0	0	0	1	57
Aunty V	0	0	0	0	1	8	0	0	0	0	0	9
Cacique	0	0	0	0	0	0	0	0	0	3	0	3
Chippy	0	0	0	0	0	1	0	0	0	0	0	1
Miss Merlin	8	0	2	1	0	0	0	11	0	6	4	32
Nina	0	0	0	0	0	1	0	7	0	0	2	10
Salvador	68	0	0	1	71	0	0	0	2	0	0	142
Soca	36	1	1	2	8	4	0	2	53	0	0	107
Stormy	58	10	0	77	7	0	0	0	0	0	2	154
Total	184	11	3	83	90	14	37	20	55	9	9	515

Table 4: Author's Classification for 2010 Whistles

Dolphin	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**G**	**H**	**I**	**J**	**Total**
Andy	2	0	0	0	2	1	2	0	0	1	0	8
Clifton	0	0	0	0	22	0	0	0	0	0	0	22
Dot	1	0	0	1	0	6	1	0	0	0	0	9
Goombay	76	0	0	0	2	0	0	0	0	0	0	78
Gussie Mae	1	0	0	0	0	0	0	0	0	0	0	1
Jake	19	0	0	0	0	1	0	0	0	0	1	21
Laguna	13	0	0	0	0	0	0	0	0	0	0	13
Salvador	8	0	0	0	19	0	1	0	1	0	0	29
Shawn	30	0	0	0	8	0	0	0	0	0	0	38
Soca	1	0	0	0	0	0	0	0	0	0	0	1
Stormy	94	14	0	84	0	0	0	0	13	0	1	206
Total	245	14	0	85	53	8	4	0	14	1	2	426

Three collaborators were asked to sort all 941 whistles into one of the 10 categories identified (Figure 2). Appendix A has additional tables (A.1-A.6) that summarize how each observer sorted the whistles for 2007 and 2010. For both years, the three whistle types that were most frequently observed were A, D, and E. In 2010, no whistles were identified as type G by any of the four collaborators while only one individual, collaborator #3, identified any whistles as type C. In order to determine inter-observer reliability for the human-based categorization system utilized here, the percentages of all whistle classifications that matched my original classification were calculated from the remaining three collaborator's arrangements. Tables 5 and 6 summarize these percentages for each of the 10 contour categories for 2007 and 2010, respectively, as well as the agreement among all whistles overall for each year.

Table 5: Percent of overall and unanimous agreement for each whistle contour type for the 2007 whistle classifications

Contour Category	**% of Total Whistle Contours that Match the Original Categorization**
A	84.2
B	90.9
C	83.3
D	88
E	76.3
Fa	92.9
Fb	78.3
G	70
H	51.8
I	55.6
J	44.4
Overall	77.7

Table 6: Percent of overall and unanimous agreement for each whistle contour type for the 2010 whistle classification

Contour Category	**% of Total Whistle Contours that Match the Original Categorization**
A	86.3
B	100
C	N/A
D	88.5
E	78.8
Fa	78.1
Fb	68.7
G	N/A
H	60.7
I	100
J	37.5
Overall	84.9

Individual-Based Variation

A Pearson's Chi-squared test was run with both an asymptotic distribution and a Monte Carlo simulation. Both cases yield similar statistic results and the null hypothesis was rejected for both 2007 and 2010 data (2007: Pearson's Chi-squared test: $X^2 = 671.05$, df = 40, p-value = <<0.01; Pearson's Chi-squared test with Monte Carlo simulation: $X^2 = 671.05$, df = N/A, p-value = <<0.01 --- 2010: Pearson's Chi-squared test: $X^2 = 464.49$, df = 54, p-value = <<0.01; Pearson's Chi-squared test: $X^2 = 464.49$, df = N/A, p-value = <<0.01). These results suggest that there is significant variation of whistle contour production between individual dolphins. Standardized residuals were used in order to determine the patterns of production for each individual dolphin (Tables 7 and 8).

Table 7: Standardized residuals indicating observed production patterns by individual for 2007. Large positive residuals indicate whistles being used more frequently than expected and are made bold in this table.

Dolphin	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**G**	**H**	**I**	**J**
Andy	-2.13	-1.21	-0.63	-2.86	-2.68	-0.73	**17.47**	-1.32	-2.85	-0.89	0.22
Miss-Merlin	-1.50	-0.88	**4.24**	-2.15	-2.75	-0.53	-1.67	**11.57**	-2.08	**9.34**	**5.47**
Salvador	**3.06**	-2.14	-1.11	-6.10	**11.71**	-1.28	-4.03	-2.33	-4.38	-1.57	-1.70
Soca	-0.91	-1.03	0.49	-4.68	-3.22	**3.81**	-3.33	-0.56	**14.23**	-1.30	-1.40
Stormy	0.08	**4.31**	-1.17	**13.25**	-5.27	-1.36	-4.27	-2.47	-5.31	-1.66	-0.16

Table 8: Standardized residuals indicating observed production patterns by individual for 2010. Large positive residuals indicate whistles being used more frequently than expected and are made bold in this table.

Dolphin	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**G**	**H**	**I**	**J**
Clifton	-5.78	-0.91	N/A	-2.46	**12.74**	-0.24	-0.24	N/A	-0.91	N/A	-0.34
Goombay	**7.68**	-1.85	N/A	-5.01	-2.96	-0.49	-0.49	N/A	-1.85	N/A	-0.69
Jake	**3.01**	-0.89	N/A	-2.40	-1.78	**4.29**	-0.23	N/A	-0.89	N/A	**2.87**
Laguna	**3.06**	-0.69	N/A	-1.87	-1.39	-0.18	-0.18	N/A	-0.69	N/A	-0.26
Salvador	-3.56	-1.05	N/A	-2.85	**8.94**	-0.28	**3.61**	N/A	0.00	N/A	-0.39
Shawn	**2.63**	-1.22	N/A	-3.30	1.67	-0.32	-0.32	N/A	-1.22	N/A	-0.45
Stormy	-5.54	**3.76**	N/A	**10.16**	-7.73	-1.01	-1.01	N/A	**3.22**	N/A	-0.02

Gender-Based Variation

When Chi-square tests and standardized residuals were run to test for gender-based whistle variation, the results yielded outcomes that are potentially more indicative of individual whistle production rather than gender-based whistle production. For example, the results from standardized residuals run on both 2007 and 2010 data suggest that male dolphins are more likely to produce type D whistles; however, when one looks at the raw data, one individual dolphin (Stormy) produced 92% and 100% of the D whistles found in the data used for the statistical tests in 2007 and 2010, respectively. Therefore, it is incorrect to say that male dolphins are more likely to produce D whistles because it is one individual male dolphin producing this whistle type more frequently than other dolphins of both genders. While it may be something to investigate in the future, the data presented here do not indicate the presence of any strictly gender-based contour variation.

Age-Based Variation

To test for any age-based variation, a Pearson's Chi-squared test was run with both an asymptotic distribution as well as a Monte Carlo simulation. Although the chi-square (2007: Pearson's Chi-squared test: $X^2 = 276.92$, df = 20, p-value = <<0.01; Pearson's Chi-squared test with Monte Carlo simulation: $X^2 = 276.91$, df = N/A, p-value = <<0.01 --- 2010: Pearson's Chi-squared test: $X^2 = 349.46$, df = 27, p-value = <<0.01; Pearson's Chi-squared test: $X^2 = 349.45$, df = N/A, p-value = <<0.01) and standardized residuals (Tables 9 and 10) suggest a significantly different pattern of production based on age groups it is possible that these patterns may be more indicative of individual variation than actual age-based variation.

Table 9: Standardized residuals indicating observed production patterns by age group for 2007. Large positive residuals indicate whistles being used more frequently than expected and are made bold in this table.

Age	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**G**	**H**	**I**	**J**
Calf	**3.90**	-2.11	-1.26	-5.31	**6.89**	-2.64	-3.97	-1.89	-2.94	0.27	0.62
Subadult	-1.48	-1.34	**2.19**	-5.33	0.05	0.25	-1.89	**2.95**	**9.01**	**2.22**	0.77
Adult	-2.22	**3.10**	-0.80	**9.56**	-6.29	**2.17**	**5.28**	-0.91	-5.36	-2.22	-1.24

Table 10: Standardized residuals indicating observed production patterns by age group for 2010. Large positive residuals indicate whistles being used more frequently than expected and are made bold in this table.

Age	**A**	**B**	**C**	**D**	**E**	**Fa**	**Fb**	**H**	**I**	**J**
Calf	-6.13	-1.10	**13.80**	-2.90	**5.97**	-1.06	-0.65	-0.95	-0.36	-0.18
Juvenile	0.34	-1.25	-1.37	-3.30	**5.17**	-0.73	0.01	-0.56	-0.40	-0.70
Subadult	**7.80**	-1.78	-1.94	-4.69	-2.27	-1.53	-1.05	-1.34	-0.04	0.23
Adult	-3.05	**2.83**	-5.31	**7.44**	-4.72	**2.28**	1.20	1.95	0.49	0.35

As with gender-based variation data, these calculations seem more indicative of individual-based variation; still, it may be possible that younger dolphins like calves and juveniles are indeed more likely to produce whistle types A and E as they are two of the more simplistic whistle contours.

Discussion

Study Subjects and Whistle Parameters

The whistles of all 16 dolphins were measured and averaged across several acoustic parameters (Tables 1 and 2). Although individual-based variations seen within these parameters were not the focal point of this study, a few patterns were observed that may suggest a possibility for future research. For example, Cacique, born in 2006 and the youngest participant in 2007, had the overall lowest average maximum frequency at 8.09 kHz. This value is more than 2 kHz lower than the next lowest average (10.27 kHz), which belonged to Miss Merlin, an adult female. Previous studies have suggested that bottlenose dolphin calves experience changes in their whistle production over their first year of life. McCowan and Reiss (1995b) recorded whistles from captive-born infant calves from birth through their first year of life and found that many whistles they produced were unique to their developmental stages resulting in a high turnover rate of whistle types produced throughout that first year. Caldwell et al. (1990) examined the whistles of 14 infant dolphins and noted that, while newborn dolphins are able to produce whistles at birth, the production patterns do not become stereotyped or predictable until some time has passed. The earliest at which they observed an infant dolphin developing a signature whistle was between 45 and 68 days (Caldwell et al., 1990). While Cacique did not produce whistles in the 2010 data set, further evaluation of whistles produced by Cacique to maturation could provide insight into whether or not his apparent use of lower frequency whistles was a result of individual production patterns or perhaps an anatomical or physiological restraint on very young dolphins.

There was significant variation in the number of whistles attributed to each of the 16 dolphins included in this study. Stormy, an adult male, was the dolphin that produced the most whistles in both years, producing 38.3% of whistles attributed to identified, individual dolphins within this study. In contrast, Gussie Mae, a juvenile female, and

Chippy, an adult female, only produced one whistle each (<1% of the total whistles used in this data). The observed difference in number of documented whistles per individual could be the result of differences in the behaviors of specific animals or may be the result of the current social state of the animal. For example, mother dolphins with young calves, like Chippy, were rarely seen without their calves on screen, which made it difficult to confirm whistle assignments to the actual vocalizer. Certain dolphins may also be less likely to vocalize around the camera than others. For example, Princess, an adult, female was often seen alone on screen but still did not produce any vocalizations that could be attributed only to her. It is also possible that data collection may have occurred during periods when these dolphins were less vocal. Previous studies have provided evidence that suggests several behavioral reasons why individual dolphins within a group may temporarily decrease the amount of vocalizations they produce. A study conducted on free-ranging dolphins in Sarasota Bay suggests that bottlenose dolphins reduce the amount of communicative vocalizations they produce when swimming in close proximity to other animals (ex. traveling groups) or when they are within visual range of other animals, as occurs frequently in captive settings (Cook et al., 2004). The existence of high ambient noise levels, although unlikely in this scenario as this study dealt with captive dolphins, has been shown to decrease the production of whistles on an individual level in free-ranging bottlenose dolphins, seemingly to reduce the likelihood of vocal masking (Quick & Janik, 2008). High ambient noise levels have also been shown to facilitate an alteration to various physical parameters of whistles produced by free-ranging dolphins (May-Collado & Wartzok, 2008).

In addition to differences in the number of whistles produced by individuals, there were also differences in the number of whistles produced with respect to gender and age categories: males were observed to produce more whistles than females and adults were observed to produce more whistles that any other age group.

Inter-Observer Reliability

The inter-observer reliability of the classification system created was tested to determine if examined whistles could reliably be placed into pre-existing categories by collaborators both naive and familiar with dolphin whistle contours. In 2007, the percent of whistle classifications that matched my original classification was 77.7% and in 2010, the percent of whistle classifications that matched my original classification was 84.9%.

While the inter-observer reliability for both years was high, there were some apparent patterns of disagreement among the observers. The most common deviations from the original classifications occurred with the more simple contour patterns; for example, it was common for one or two collaborators to mark a whistle that was originally categorized as type A, as a type E or vice versa. Type E and H whistles were also often confused with one another. This suggests that perhaps the original categories were not distinct enough for observers to differentiate between, or it is possible that the categorization instructions were not sufficiently clear for observers to make consistent selections. This may be evidenced by only one observer marking 22 whistles as type C (2010) while all other collaborators identified those same whistles as type E.

Previous studies and analysis of quantitative alternatives to the human-observer method of classification suggest that it is one of the most accurate means of categorizing whistles based on overall contour shape (Janik, 1999). While it is relatively easy for software programs to measure the physical parameters of a whistle, Janik (1999) suggests that these methods are less consistent in their grouping of contour shape when compared to human assessment. Sayigh et al. (2007) compared quantitative and human-based categorization methods with results indicating quantitative methods (e.g., McCowan, 1999) are less accurate at grouping whistles based on individual vocalizer than human judges. Sayigh et al. (2007) pooled 20 random whistles from 20 different dolphins whose whistles had been recorded during a brief capture and release experiment in Sarasota Bay, Florida. They asked 10 human observers to sort the whistles into groups and discovered that the observers consistently grouped the whistles according to individual vocalizer identity. The quantitative method developed by McCowan was highly inaccurate at grouping whistles based on the vocalizers identity (Sayigh et al., 2007).

Overall, the agreement between the three collaborators with my original classification was high enough to justify the use of the classification system created for this study for the purpose of statistical examination.

Individual-Based Variation

Data collected and analyzed from 2007 suggests that each of the five included dolphins were more likely to produce certain whistle types than any of the other four dolphins (Table 7). This ability to statistically assign specific contour types to individual dolphins within the study population provides support for the signature whistle hypothesis. Previous studies conducted on both captive and free-ranging bottlenose dolphins have provided support for this premise as well. In their review of the signature whistle, Caldwell et al. (1990) summarize their decades of research on the subject in which they examined samples of whistles from 120 individual captive dolphins for percent stereotypy (a.k.a percent of whistles produced that were signature whistles). What they found was that the average percent of stereotyped whistles produced among all individuals was 94% (Caldwell et al., 1990). Another study conducted on captive bottlenose dolphins found similar results suggesting that as many as 80-90% of the whistles produced by an individual dolphin are that dolphin's signature whistle (Agafonov & Panova, 2012). The results presented in the current study suggest a smaller proportion of signature whistles produced. The percent of the statistically assigned whistle contour created by each dolphin relative to the total number of whistles they produced in 2007 are as follows: Andy – 64%; Miss Merlin – 71%; Salvador – 97%; Soca 53%; Stormy – 56%. These results average to a mean production of 68.2% signature whistles in 2007. This difference in observed proportions of signature whistle production could be the result of different methodologies utilized during the data collection process. Previous studies have provided evidence for the idea that signature whistles carry identity information and are used as a means to maintain contact with conspecifics when they are separated from each other (King & Janik, 2013; Sayigh et al., 1999; Smolker et al., 1993; Watwood et al., 2005), therefore one may expect to see an increase in the production of these whistles during experiments where forced, temporary isolation from a group is utilized as a means of accurately attributing whistles to certain individuals. Perhaps the most convincing evidence that supports the hypothesis that the unique contour shape of each whistle carries the information about the vocalizer's identity can be found in a study conducted on bottlenose dolphins in which the "voice" characteristics of the signature whistles were removed creating synthetic whistles that only matched the original whistles for frequency modulation patterns (Janik et al., 2006). This study found that dolphins continued to respond more strongly to playbacks of synthetic whistles that were reproductions of the whistle contours utilized in their relatives' signature whistles.

Data from 2010 suggested a slightly different trend with several dolphins producing a significant number of whistle types A and E (Table 8) suggesting the potential for a shared whistle repertoire in which multiple dolphins produce similar whistle contour types. Although it is possible that the smaller sample sizes of whistles per individual documented in 2010 could play a role in this observed difference as smaller sample sizes are less likely to be representative of a dolphins complete whistle repertoire, it is also possible that this observation is indicative of the fact that more simplistic whistle contour types like A, E and H (typically referred to in the literature as "upsweep" style whistles) also play an important role in bottlenose dolphin communication. McCowan and Reiss (1995a; 2001) conducted experiments on captive bottlenose dolphins from which they determined that these upsweep style whistles are the whistles that are often produced most frequently by dolphins and that the voice characteristics of those whistle are likely what help conspecifics identify who the vocalizing individual is. The results presented within the current study do not support the notions put forth by this whistle repertoire hypothesis as the data from 2007 clearly suggests the existence of signature whistle contour patterns; however, the data from 2010 do provide evidence that supports the idea that upsweep type whistles like A and E can also be produced in relatively high frequency and therefore are probably important to bottlenose dolphin communication as well. A study conducted on free-ranging bottlenose dolphins in Sarasota Bay Florida reported that roughly 52% of the whistles produced by free-ranging dolphins are signature whistles but that as much as 19% of the other whistles produced by this group of dolphins can be classified as upsweep style whistles (Cook et al., 2004). Cook et al. suggest that their results indicate that upsweep style whistles probably play an important role in communication but further research is needed shed light on what role they play.

Gender-Based Variation

The 2007 data suggests that males produce primarily A and D type whistles while females produce statistically more C, Fa, G and H whistles. However, when one looks at the raw data, many of these contour patterns are being produced by individual animals rather than multiple animals of the same gender. For example, in 2007: Salvador produced 78% of the total number of type E whistles; Stormy produced 92% of the total number of type D whistles; and Soca produced 94% of the total number of type H whistles. This suggests that gender-based whistle variation is not strong in this dolphin group as compared with the patterns produced by individuals.

The most interesting variation in whistle production that was observed between male and female dolphins was in the number of whistles produced by each group. Male dolphins were observed to vocalize 2.2 times more often than female dolphins in 2007 and 16.8 times more often than female dolphins in 2010. Despite the fact that males produced more whistles than females throughout this study, the number of total minutes of video footage obtained with female dolphins in the group was higher than the number of minutes with male dolphins in the group. In 2007, there were 12 recorded sessions (totaling around 287 minutes of video) that included at least one female in the group and 10 recorded sessions (totaling around 292 minutes of video) that included at least one male in the group. Of the 292 minutes of recorded video from 2007 containing at least one male, 134 of those minutes were from sessions that contained primarily females with one male calf present in the group. Very few whistles were attributed to this calf (Cacique) and as such, the majority of the whistles attributed to males from the 2007 data occurred during the 158 minutes of video that were recorded during sessions that contained only male dolphins. In 2010, there were 8 recorded sessions (totaling around 178 minutes of video) that included at least one female in the group and 6 recorded sessions (totaling around 146 minutes of video) that included at least one male in the group. Of the 6 sessions containing at least one male, only three of those sessions consisted of only male dolphins with the other three sessions containing primarily female participants plus the male dolphin Stormy. Even taking into account the multiple sessions in which Stormy or Cacique were the only males present in the group, the number of minutes of recorded video in which at least one male was present was lower in 2010 and roughly the same in 2007 as the number of minutes analyzed with at least one female present. These results would suggest that the overall number of minutes of video recorded within groups containing males versus females is not the underlying reason for such high amounts of observed male vocalization. Instead, this observed difference in number of vocalizations could be indicative of a tendency for male dolphins to produce a higher quantity of whistles than female dolphins for this particular dolphin group.

Age-Based Variation

For the 2007 data, standardized residuals suggested the following patterns of use based on age groups: calves produce mostly A and E type whistles; sub-adults produce mostly C, G, H and I type whistles; and adults produce B, D, Fa and Fb type whistles. For the 2010 data, the following patterns of use were determined using standardized residuals: calves produce C and E type whistles; juveniles produce E type whistles; sub-adults produce A type whistles; and adults produce B, D and Fa type whistles. These proposed patterns of use are likely skewed by individual production. For example, Stormy, who is an adult, produced 100% of the type D whistles in 2010, therefore, it is fundamentally inaccurate to state that these data suggest that adults are more likely to produce type D whistles when only one individual adult was observed to create that contour type. As such, it can be stated that data presented here do not indicate the existence of specific age-based contour variation in bottlenose dolphins. However, the data do suggest a possible tendency for increased whistle contour complexity with increased age. Previous studies suggested that whistle contours observed to be unique to individual dolphins were also unique to the life stage of that dolphin meaning that signature whistles may evolve over the animal’s life-span (McCowan & Reiss, 1995b). It is possible that younger dolphins are more likely to produce sequences of simpler whistle contours, like types A and E, while adult dolphins are more likely to produce complex, multi-inflection whistles. Caldwell et al. (1990) discussed their observed various changes to whistle production even after the initial development of the signature whistle occurs. Some of these changes included; an increase in number of loops utilized per whistle, longer durations and higher amounts of frequency modulation as the dolphins aged. Long-term evaluation of the whistles produced by the dolphins used in the current study might shed light on the potential evolution of signature whistles for individual dolphins.

Whistle Consistency – 2007 and 2010

In the current study, only two dolphins produced enough whistles in both 2007 and 2010 for consistency between years in their calls to be examined. Stormy produced whistle types B and D in both years. Though only three years apart, Stormy's consistency in producing both B and D call types supports the notion that bottlenose dolphins maintain stereotyped whistles over time. Previously conducted studies have suggested that bottlenose dolphins are capable of maintaining their signature whistle contour for long periods of time for the proposed purpose of being able to recognize individuals after extended periods of separation as is common in a fission-fusion society (Bruck, 2013; Caldwell et al., 1990; Sayigh et al., 1990).

In 2007, Salvador produced more A and E whistles than could be expected by chance; in 2010, he only produced type E whistles more frequently than could be expected by chance. Salvador's apparent discontinued use of type A whistles could have resulted from a skewed sample of his calls or might be related to the large difference in whistle sample sizes per year for him. More whistles were documented from Salvador in 2007 (N=142) than in 2010 (N=29). One explanation is that whistles included from 2007 were a better representation of his repertoire than the much smaller sample size from 2010. Still, it is possible that the observed differences in Salvador's whistle patterns are related to the development of his signature whistle with age. This notion is supported by the fact that in 2007, Salvador produced 1.04 type E whistles for every type A whistle, while in 2010, that number increased to 2.37 type E whistles for every type A he produced. Further analysis of an additional sample of Salvador's whistles may help elucidate if the observed differences between 2007 and 2010 were representative of the evolution of his whistle production patterns or a product of a smaller sample size of whistles available for him in 2010.

Considerations for Future Research

While the results presented in the current study did not support contour pattern variation by gender or age, it is possible that other whistle characteristics (e.g., frequency and duration) may vary based on dolphin age or sex. Future research could look for potential gender or age differences in whistle parameters; e.g., maximum frequency, duration, number of loops in a whistle or sequence, etc. Future research could also examine the tendency observed within this study for males to produce a larger quantity of whistles than female dolphins. Future examination of the whistle characteristic production capabilities of infant calves could shed light on limiting parameters such as frequency and octave ranges and how those limitations change during development.

Although support for the accuracy of human categorization as a means of sorting whistle spectrograms based on contour shape has been supported by previous studies (Janik, 1999; Sayigh et al., 2007) and the current study, future development of a reliable quantitative means of sorting whistles based on contour shape could help illuminate patterns within the contours that escape human recognition. A quantitative approach to whistle analysis could also prove important in the effort to determine the communicative use of common non-signature whistles like the upsweep style whistles.

Results from this study suggest that these bottlenose dolphins possess individually distinct contour patterns – signature whistles. During the course of whistle analysis, sequences containing multiple whistles of the same contour pattern from individual dolphins were noted. Figure 3 is an example of a typical sequence produced by Stormy who often created several D type whistles in a row with similarly spaced breaks between each whistle. Future studies could examine sequences like these to better understand how their use by dolphins might vary by individual, behavior or interaction.

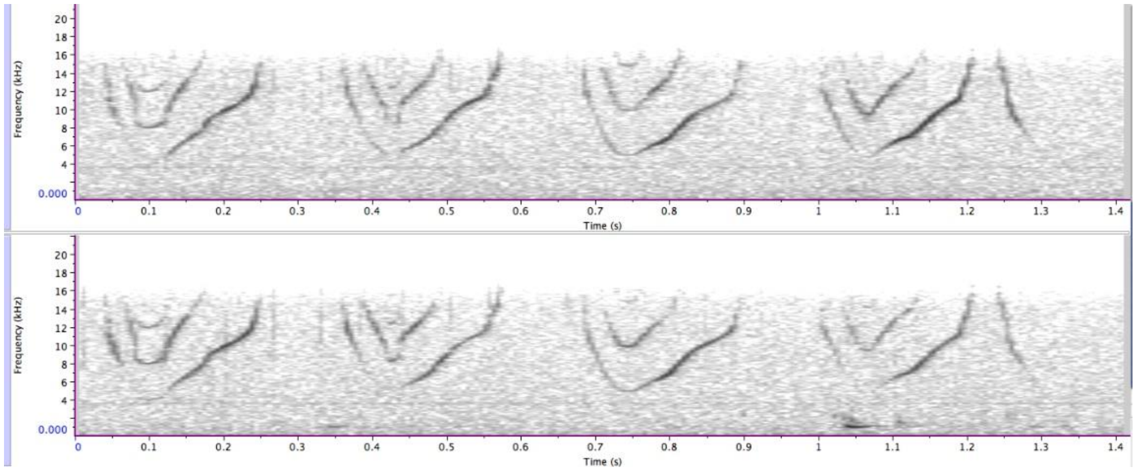


Figure 3: An example of a typical sequence of whistles produced by Stormy

An additional consideration for conducting future research is the recording specifications of the equipment. While the hydrophones used for the data collection in this study were able to capture most whistle contours completely, the shape of type G whistles were likely the result of whistles being "clipped" by the upper frequency limits of the recording devices. The recording equipment utilized within this study captured sound frequencies up to around 15 kHz. By increasing the upper frequency limit to 24 kHz, an amount that would include the highest points of fundamental frequencies observed by several other bottlenose dolphin whistle production studies (Caldwell et al., 1990; Madsen et al., 2012; May-Collado & Wartzok, 2008), a more complete spectrographic image of the whistle contours may be achieved.

Conclusions

Individual recognition is carried out through chemical, visual or acoustic means for various reasons within the animal kingdom including kin recognition, mother-calf reunions and mate location. (Kondo & Izawa, 2014; Passos et al., 2013; Shapiro, 2010; Speed, 2000; Wyatt, 2010). Recognition via acoustic means is often carried out through the use of signature vocalizations which are individually unique signals used to portray information about vocalizer's identity to surrounding conspecifics. Signature vocalizations are used by various terrestrial (Marchant-Forde et al., 2002; Terrazas et al., 2003; Torriani et al., 2006) and marine animals (Charrier et al., 2010; Halliday, 1990; Riesch et al., 2006; Van Opzeeland & Van Parijs, 2004) to facilitate mother-calf reunions and maintain social structure within group-dwelling animals. Bottlenose dolphins, along with many other delphinid species, utilize frequency-modulated whistles for the purpose of acoustic communication with conspecifics (May-Collado & Wartzok, 2008; Reiss et al., 1997). Whistles are produced by vibrating tissue in the nasal cavity (Madsen et al., 2012). There is some debate as to when whistle repertoires are developed with some research suggesting that preliminary repertoires, that include an individually unique signature whistle, are developed within the first year of life (Caldwell et al., 1990) while other research suggests no such signatures vocalization has been developed by the end of that first year (McCowan & Reiss, 1995b). Vocal learning plays an important role in the development of an individual dolphin's whistle repertoire (Miksis et al., 2002; Reiss & McCowan, 1993; Ridgway et al., 2012; Watwood et al., 2004; Weiss et al., 2006). Whistle use changes in different behavioral and environmental contexts (May-Collado & Wartzok, 2008; Quick & Janik, 2008) and may have temporal and structural patterns (Cancho & McCowan, 2012; Nakahara & Miyazaki, 2011). Alterations to an individual dolphin's normal whistle patterns may be indicative of a distressed status (Caldwell et al., 1990; Esch et al., 2009; Herzing, 1996; Lopez, 2011) and the copying of another dolphin's signature whistle may be used to maintain contact between closely bonded individuals during periods of separation (King & Janik, 2013; King et al., 2013). The two main hypotheses dealing with the existence/use of signature whistles are the signature whistle hypothesis (Caldwell et al., 1990) and the whistle repertoire hypothesis (McCowan & Reiss, 1995a).

Empirical evidence suggests that bottlenose dolphins use signature whistles to share information about their identity, and possibly their location, with surrounding conspecifics (Caldwell et al., 1990; Janik et al., 2006; Sayigh et al., 2007; Smolker et al., 1993; Watwood et al., 2005). The original research portion of my Capstone supports the existence of stereotyped whistle contours produced by individual dolphins at Dolphin Encounters. In addition to the production of individually unique signature whistles, previous studies have also suggested that simple upsweep style whistles probably play an important role in dolphin communication (Cook et al., 2004; McCowan & Reiss, 1995a). The current study also provides some evidence for the relatively frequent production of these whistles and therefore the probable importance of these whistles in bottlenose dolphin communication. Therefore, the data presented with the original study of this work provide support for aspects of both the signature whistle hypothesis and whistle repertoire hypothesis. Although most empirical evidence to date provides support for the hypothesis that signature whistle contours carry identity information about the vocalizing individual, future research could shed light on the potential use(s) of the upsweep style whistles.

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Appendix A: Collaborator Reliability Classification Tables

Table A.1: Collaborator #1's Classification for 2007 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	13	0	1	1	13	1	26	0	0	0	2	57
Aunty V	0	0	0	0	1	8	0	0	0	0	0	9
Cacique	0	0	0	0	0	0	0	0	0	3	0	3
Chippy	0	0	0	0	0	1	0	0	0	0	0	1
Miss Merlin	9	0	2	1	0	0	0	11	0	2	7	32
Nina	0	0	0	0	0	0	0	6	0	0	4	10
Salvador	60	0	0	0	75	0	0	0	1	0	6	142
Soca	46	1	1	1	41	4	0	2	9	0	2	107
Stormy	57	10	0	79	8	0	0	0	0	0	0	154
Total	185	11	4	82	138	14	26	19	10	5	21	515

Table A.3: Collaborator #2's Classification for 2007 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	17	0	1	3	6	0	28	0	0	0	2	57
Aunty V	0	0	0	0	1	8	0	0	0	0	0	9
Cacique	2	0	0	0	1	0	0	0	0	0	0	3
Chippy	0	0	0	0	0	1	0	0	0	0	0	1
Miss Merlin	6	0	4	1	2	2	3	9	1	2	2	32
Nina	0	0	0	0	0	0	3	7	0	0	0	10
Salvador	67	0	0	9	64	0	0	0	2	0	0	142
Soca	13	1	1	1	26	4	1	2	58	0	0	107
Stormy	45	10	0	72	25	0	0	0	0	0	2	154
Total	150	11	6	86	125	51	35	18	61	2	6	515

Table A.4: Collaborator #3's Classification for 2007 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	16	0	1	1	10	3	25	0	0	0	1	57
Aunty V	0	0	0	0	1	8	0	0	0	0	0	9
Cacique	2	0	0	0	0	0	0	0	0	1	0	3
Chippy	0	0	0	0	0	1	0	0	0	0	0	1
Miss Merlin	9	0	2	1	0	2	11	0	0	4	3	32
Nina	0	0	0	0	0	2	7	0	0	0	1	10
Salvador	87	0	0	1	38	0	0	2	1	1	12	142
Soca	42	1	0	1	47	5	3	0	4	2	2	107
Stormy	63	8	0	65	12	4	1	0	1	0	0	154
Total	219	9	3	69	108	25	47	2	6	7	19	515

Table A.6: Collaborator #1's Classification for 2010 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	1	0	0	0	2	0	2	0	1	1	1	8
Clifton	0	0	0	0	22	0	0	0	0	0	0	22
Dot	1	0	0	1	0	7	0	0	0	0	0	9
Goombay	75	0	0	0	1	0	0	0	0	0	2	78
Gussie Mae	1	0	0	0	0	0	0	0	0	0	0	1
Jake	19	0	0	0	0	1	0	0	0	0	1	21
Laguna	13	0	0	0	0	0	0	0	0	0	0	13
Salvador	9	0	0	0	19	0	1	0	0	0	0	29
Shawn	35	0	0	0	3	0	0	0	0	0	0	38
Soca	1	0	0	0	0	0	0	0	0	0	0	1
Stormy	101	14	0	77	2	0	0	0	10	0	2	206
Total	256	14	0	78	49	8	3	0	11	1	6	426

Table A.7: Collaborator #2's Classification for 2010 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	0	0	2	0	1	1	2	0	0	1	1	8
Clifton	0	0	16	0	6	0	0	0	0	0	0	22
Dot	0	0	0	1	0	0	7	0	1	0	0	9
Goombay	54	0	0	0	21	0	0	0	1	0	2	78
Gussie Mae	0	0	0	0	1	0	0	0	0	0	0	1
Jake	14	0	0	0	5	2	0	0	0	0	0	21
Laguna	9	0	0	0	4	0	0	0	0	0	0	13
Salvador	9	0	0	0	18	1	0	0	1	0	0	29
Shawn	6	0	0	0	32	0	0	0	0	0	0	38
Soca	1	0	0	0	0	0	0	0	0	0	0	1
Stormy	51	14	0	88	34	13	2	0	1	0	3	206
Total	144	14	18	89	122	17	11	0	4	1	6	426

Table A.8: Collaborator #3's Classification for 2010 Whistles

Dolphin	A	B	C	D	E	Fa	Fb	G	H	I	J	Total
Andy	0	0	0	0	2	2	1	0	0	2	1	8
Clifton	0	0	0	0	21	0	0	0	0	0	1	22
Dot	1	0	0	1	0	7	0	0	0	0	0	9
Goombay	76	0	0	0	0	1	0	0	0	1	0	78
Gussie Mae	1	0	0	0	0	0	0	0	0	0	0	1
Jake	19	0	0	0	0	1	1	0	0	0	0	21
Laguna	13	0	0	0	0	0	0	0	0	0	0	13
Salvador	14	0	0	0	14	1	0	0	0	0	0	29
Shawn	32	0	0	0	4	0	0	0	0	0	2	38
Soca	1	0	0	0	0	0	0	0	0	0	0	1
Stormy	82	14	0	73	17	7	0	0	13	0	0	206
Total	239	14	0	74	58	19	2	0	13	3	4	426