The University of Southern Mississippi

The Aquila Digital Community

Dissertations

Fall 12-1-2017

Cetacean Exhalation: An Examination of Bottlenose Dolphin (*Tursiops truncatus*) Use of Three Bubble Production Types through Associated Behaviors

Kelsey Moreno
University of Southern Mississippi

CETACEAN EXHALATION: AN EXAMINATION OF BOTTLENOSE DOLPHIN *(TURSIOPS TRUNCATUS)* USE OF THREE BUBBLE PRODUCTION TYPES THROUGH ASSOCIATED BEHAVIORS.

by

Kelsey R. Moreno

A Dissertation
Submitted to the Graduate School,
the College of Education and Psychology,
and the Department of Psychology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

December 2017

CETACEAN EXHALATION: AN EXAMINATION OF BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) USE OF THREE BUBBLE PRODUCTION TYPES THROUGH ASSOCIATED BEHAVIORS.

by Kelsey R. Moreno

December 2017

Approved by:

Dr. Donald Sacco, Committee Chair
Assistant Professor, Psychology

Dr. Lauren Highfill, Committee Member
Associate Professor, Psychology, Eckerd College

Dr. Richard S. Mohn, Committee Member
Associate Professor, Educational Research and Administration

Dr. Alen Hajnal, Committee Member
Associate Professor, Psychology

Dr. Joe Olmi
Chair, Department of Psychology

Dr. Karen S. Coats
Dean of the Graduate School

Published by the Graduate School

THE UNIVERSITY OF SOUTHERN MISSISSIPPI®

ABSTRACT

CETACEAN EXHALATION: AN EXAMINATION OF BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) USE OF THREE BUBBLE PRODUCTION TYPES THROUGH ASSOCIATED BEHAVIORS.

by Kelsey R. Moreno

December 2017

Bubble production through exhalation is unique to marine mammals due to the combination of their air-breathing physiology and aquatic environment. Multiple types of bubble production are reported in the literature, including bubble netting, trails, bursts, and rings. Unfortunately, apart from bubbles produced to facilitate hunting or play, current understanding of the function of bubble production in cetaceans is limited to anecdotal accounts and author interpretations. This study aims to identify the function of three bubble types though observations of behaviors present before, during, and after bubble production. Instances of bubble trails, bubble bursts, and scant bubbles were selected from underwater video observation of bottlenose dolphins in human care. Rates of behaviors before, during, and after bubble production were recorded for each individual present during a bubble event, along with the individual's age, sex, and role as bubbler or bystander. Suites of observed behaviors were grouped by function for analyses. Logistic regressions were used to determine which behavioral factors and demographics predicted bubble production across time periods for different bubble types. Predicting behaviors for bubble trail production showed use in multiple social situations. Behaviors predicting bubble burst production indicated use in avoidance, sexual behavior, object engagement, and as early exhalation during surfacing. Scant bubble production predictive behaviors demonstrated use in close proximity social behavior and non-social interest. These results provide a better understanding of how bubble production types fit into the behavioral repertoire, which supports some previously suggested behavioral uses of bubble production, and provides future research on bubble production directions to explore. By identifying these differences in behavioral patterns, we can better identify the function of bubble behaviors and how they fit into the bottlenose dolphin behavioral repertoire. Ultimately, this will enable us to better interpret bubble behaviors, benefiting future experimental and observational studies interested in behavioral responses of bottlenose dolphins.

ACKNOWLEDGMENTS

First and foremost, I would like to thank Riley Macgregor for her extensive work identifying bubble events and coding behaviors. This project would never have existed without Audra Ames; I am so grateful for our engaging discussions which sparked the idea for this study. I am grateful to Diana Reiss for her suggestion to investigate artiodactyl startle responses and their connection to bubble burst behavior. A huge thank you to Stan Kuczaj for supporting the initial development of the project idea and providing video data for analysis. I am indebted to Teri and Eldon Bolton and the rest of the Roatan Institute for Marine Sciences staff for being wonderful to work with and allowing us to film their animals. Thank you to Laura Misson for her extensive time and work selecting bubble events, Ali Taylor and Erin Frick for their aid in the early stages of the project, Sarah Saltiel for her assistance in entering behaviors for reliability calculations, and Tabatha Lewis for her assistance prepping data for analysis. I am incredibly grateful to Rich Mohn for his statistical consultations and quick thinking when my data did not look as anticipated. Thank you to the rest of my wonderful dissertation committee, Lauren Highfill, Don Sacco, and Alen Hajnal, for their suggestions and enthusiastic support. Finally, thank you to David Echevarria for ensuring I could complete this project.

DEDICATION

To all of the animals in my life. Thank you for inspiring me every day.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I – INTRODUCTION

Bubble Production in Marine Mammals

Bubble production through exhalation is a behavior characterized by the release of air from the respiratory system while underwater. As marine mammals are the only air-breathing animals which spend a majority of their time underwater, they possess the unique combination which enables them to make greater use of bubble behavior. While only a few reports of bubble production in pinnipeds exist (Boness, Bowen, Buhleier, & Marshall, 2006; Merdsoy, Curtsinger, & Renouf, 2010), the literature is peppered with reports of bubble production in multiple species of cetaceans.

Bubbles themselves can take of a range of forms and serve a variety of functions. One of the more well documented uses of bubble productions is as a component of foraging. Of these, the most iconic is likely bubble netting in humpback whales (Hain, Carter, Kraus, Mayo, & Winn, 1981; Sharpe & Dill, 1997; Wiley et al., 2011), wherein the whales contain prey inside circular curtains of bubbles before lunging through the middle. Similarly, bottlenose dolphins have been recording using bubble bursts in conjunction with other herding behaviors to keep fish at the water surface and increase ease of prey capture (Fertl & Wilson, 1997; Fertl & Würsig, 1995). This behavior has also been observed in mixed species feeding aggregations containing bottlenose dolphins and false killer whales (Zaeschmar, Dwyer, & Stockin, 2013). A different form of bubble use in foraging has been observed in orcas, which created turbulence near the edge of an ice flow by blowing bubbles (Visser et al., 2008). In contrast to the practical function of bubbles produced during foraging, bubbles may also be created and then used as a manipulatable object during play, particularly in captive settings, (e.g.: Delfour &

Aulagnier, 1997; Jones & Kuczaj, 2014; McCowan, Marino, Vance, Walke, & Reiss, 2000; Paulos, Trone, & Kuczaj, 2010).

There are additionally many instances of bubbles which have no apparent physical function. Most authors agree that these bubbles are likely used as a communication signal (Herzing, 2000; Pryor, 1990), however, what little is known about their function is limited to author interpretations of observational instances. Fortunately, these reports have begun to catalogue multiple forms of bubble productions, allowing for identification of different characteristic structures. Currently, the commonly recognized bubble types are bubble trails, bubble bursts, and bubble rings.

Bubble Trails

Behavioral use

One of the most common bubble production types takes the form of a long, thin stream of bubbles. These can be single streams, or multiple visually distinct streams separated by very short time intervals which together constitute a bout (Beard, 2007). Most commonly called bubble trails, the terms bubble streams and whistle trails are also used. While these terms are generally used interchangeably, some sources separate terms based on bubble patterning or separation, or presence of whistles.

Bubble trails are predominantly observed in social situations (Beard, 2007; Dudzinski, 1998; Herzing, 1996; Pryor, 1990), particularly in groups with multiple individuals producing bubble trails (Beard, 2007), indicating they are communicative signals. Use of visual signals in cetaceans is well-established (Caro, Beeman, Stankowich, & Whitehead, 2011), so we know dolphins have the perceptual ability to communicate in this manner. Additionally, observations of bubble trails during distress events (Kuczaj et al., 2015), aggressive behavior (Dudzinski, 1998), behavioral settings labeled as high emotion, and synchronized whistles (Herzing, 1996) supports this usage. Further support for the use of bubble trails as visual signals comes from their common association with whistles. As adult dolphins are able to vocalize without expelling air (Mackay & Liaw, 1981; Pryor, 1990), the often observed relationship of bubble trails with whistles (Herzing, 1996; Pryor, 1990) and other vocalizations (van der Woude, 2009; Wood, 1953) may indicate a tandem function, perhaps for emphasis or source localization (Pryor, 1990). Moreover, production frequency differs by sex and age class, with females producing more bubble trails than males, subadults producing more than juveniles, which produced more than adults, which produced more than calves; and most bubble trails were produced in the presence of the calf (Beard, 2007).

Connection with vocalizations

The common association between bubble trails and whistles has also led to debate over methodological uses of bubbles to identify vocalizing individuals, particularly with respect to whether bubble trail whistles are representative of the whistle repertoire. Current methodology uses bubble trails to isolate whistles and identify which individual is vocalizing (Ames, 2016; Herzing, 2000; McBride & Kritzler, 1951). This is especially useful for young calves with little motor control, who emit bubble trails as part of vocalizing (Gnone & Moriconi, 2009; McCowan & Reiss, 1995b). However, there is a great deal of debate over whether it is appropriate to use bubble trails to isolate the vocalizing individual (Ames, 2016; Fripp, 2005, 2006; McCowan, 2006), particularly in adults. One argument is that bubble trails with whistles are representative of the vocal repertoire because there is no difference between whistle-types produced with and without bubbles (McCowan & Reiss, 1995a). Conversely, evidence of bubble trail whistle context dependence, typical clustering of bubbles trails, occurrences of bubble trails not associated with all whistle types, and greater probability of bubble trail occurrence when a calf is present or when a calf is separated from its mother suggests bubble trails convey additional information and may be correlated with particular behavioral states (Fripp, 2005, 2006). Both perspectives agree that the relationship of bubble trails to whistle types, behavioral states, and affective states, as well as the reason for bubble trail use is currently unclear (Fripp, 2005, 2006; McCowan, 2006; McCowan & Reiss, 1995a).

Bubble Bursts

Another common form of bubble production is the sudden release of a large amount of air resulting in a cloud-like clustering of bubbles. Various sources refer to this as either the bubble burst or bubble cloud; however, some sources use both terms to denote separate, ambiguously defined categories. While a range of studies have reported bubble bursts, knowledge of their function is limited. The most commonly accepted functions of bubble bursts are as a threat or a response to a surprise or aversive stimulus; conclusions which are generally supported by anecdotal data.

One possible use of bubble bursts is as a threat or other aggressive signal. Bubble bursts have been demonstrated to occur more often during group orientation changes, leading the authors to conclude this was due to aggression during disagreements over decision making (Lusseau, 2006). Further support comes from experimental tests on the response of marine mammals to simulated fishing gear and pingers; California sea lions, Commerson's dolphins, and bottlenose dolphins emitted bubble bursts along with agonistic behaviors to these aversive stimuli, indicating the bursts may also be aggressive in nature (Bowles & Anderson, 2012). Bursts have also been observed in the wild in conjunction with aggressive behaviors in Atlantic spotted dolphins (Dudzinski, 1998). Belugas also appear to use bubble bursts as an agonistic behavior (Hill, 2009), particularly in defense of their calves or as a possible warning during social interactions (Hill et al., 2011).

Other sources claim bubble bursts are indicative of surprise, excitement, or curiosity (Marten, Shariff, Psarakos, & White, 1996; McCowan et al., 2000), with one source dubbing the behavior a "query balloon" to reflect this usage (Pryor, 1990). This interpretation is supported by responses to objects during experimental studies. Both a mirror test with orcas and false killer whales (Delfour & Marten, 2001) and an underwater maze device for bottlenose dolphins (Clark, Davies, Madigan, Warner, & Kuczaj, 2013) elicited bubble bursts from the study subjects. However, only one study so far has demonstrated significantly more bubble burst production in response to a surprising stimulus than a control (Lilley, 2017). It is important to note that these uses are not necessarily mutually exclusive, and that bubble bursts may serve both functions. The only proposed exception to these functions is one report of bubble bursts produced during courtship behavior in spotted dolphins (Herzing, 1996).

Additionally, there is evidence the bubble burst may be derived from a common artiodactyl behavioral response. A snort consists of a short, forceful exhalation of a large amount of air, which, if produced underwater, would take the form of a bubble burst. Snorts, and variations of the sort, are common behaviors among a range of artiodactyl species indicating it is likely phylogenetically retained (Cap, Deleporte, Joachim, &

Reby, 2008; Kiley, 1972). While there is debate over the exact relationship of Cetacea to other Artiodactyla clades (Gatesy & O'Leary, 2001; Thewissen, Cooper, Clementz, Bajpai, & Tiwari, 2007), it is commonly accepted that Cetacea either falls within Artiodactyla (Boisserie, Fisher, Lihoreau, & Weston, 2011; Graur & Higgins, 1994; O'Leary & Gatesy, 2008) or shares a common ancestor with the group (Thewissen, 1994), and thus a comparison is useful for understanding evolutionary behavioral development.

The function of snorts and similar behaviors varies by species, though use is typically reactionary in nature and related to alarm, danger, (Caro, Graham, Stoner, & Vargas, 2004; Stankowich & Coss, 2007) startle, or unfamiliar objects or situations (Kiley, 1972). Deer use snorts for a range of functions including alarm, agonistic, dominance success, predator defense, and territorial calls (Cap et al., 2008). Tapirs snort in aggressive situations (Kiley, 1972). Snorting is classified as a fear behavior in horses (Leiner & Fendt, 2011), and is also observed when they investigate a strange object (Kiley, 1972). Another variation is seen in the rhinoceros, which uses a vocalization derived from the snort, a whistle, as a contact call. These functions all bear similarity to the proposed functions of bubble bursts, suggesting the reports of burst use have been correct in their interpretations of this behavior.

Bubble Rings

The third commonly reported type of bubble production is the bubble ring, a release of air which forms a single, unbroken torus. Unlike bubble trails and bursts, rings are commonly discussed in association with play behaviors, and most reports are of cetaceans producing and then manipulating the rings. Bubble ring play has been observed in multiple species, including belugas (Hill, 2009) and bottlenose dolphins (Marten et al., 1996; McCowan et al., 2000; Paulos et al., 2010). In addition to bubbles produced through exhalation of interest to this study, bubble rings can be produced by physical means, such as fluke slaps (Pace, 2000) or trapping air in the mouth (Gewalt, 1989). As is expected for play, bubble ring production is commonly followed by various manipulations and interactions with the bubbles (Gewalt, 1989; Marten et al., 1996; Pace, 2000; Paulos et al., 2010). Bubble play behaviors are also used as evidence of higher lever cognitive abilities such as creativity and planning behavior in dolphins (McCowan et al., 2000). While these examples are intriguing, it is important to note that bubble play is not a common form of play, and is generally observed in captive, not wild, populations (Paulos et al., 2010). Bubble rings are not present in the current study, which may be due to population or housing situation differences.

Despite the prevalence of reports on bubble ring play, not all bubble ring productions are used in this manner. Bubble rings have also been observed in spotted dolphins concurrently with behaviors commonly considered to be aggressive such as head-to-head displays, open mouth postures, body charges, and tail slaps to the head, particularly between males (Herzing, 1996). Similarly, other sources note the presence of bubble rings during dominance disputes (Pryor, 1990) or contexts labeled as annoyance (Herzing, 2000). Thus, it currently cannot be stated that bubble rings serve a single function, and it is likely they are used for different purposes depending on the species, population, and living situation of the bubble producer.

Scant Bubbles

In our dataset, we also noted the presence of a small, single, barely noticeable emission we term the "scant bubble". Only one previous report bears similarity to this bubble type; it is a passing mention of single bubbles, though the size is not mentioned and they are limped with other bubble types. These single bubbles were reported during aggressive exchanges in spotted dolphins (Dudzinski, 1998). However, it is possible these bubbles are of the same form as the large single bubbles reported elsewhere during a social context (McCowan et al., 2000). If so, we are the first to report the scant bubble type, likely due to the difficulty of detecting a scant bubble, particularly if not in proximity to the emitter.

Current Study

Summary

The current study aims to identify function of three bubble production types: bubble trails, bubble bursts, and scant bubbles. This was achieved though identifying patterns in associated behavior presence across time periods before, during, and after bubble production types for bubble producers and other present individuals. Additionally, age and sex of bubble producers and other present individuals was considered to determine if demographic qualities alter the use of bubble production types.

As distinct types of bubble production likely serve different behavioral functions, I expected to find different effects for each bubble type. Bubble trails have been proposed to serve as communicative signals which emphasize or alter vocal information or assist in vocal localization. Accordingly, I expected a large portion of social behaviors to occur during bubble trail events. If bubble trails are used as a visual signal, there should be a change in behaviors across time periods, whereas if bubble trails are used for emphasis or localization, a change in behavior may not occur. As we could not incorporate vocal information due to the lack of acoustical localizing methods and the presence of multiple animals within auditory range at any given time, we could not specifically address the relationship of bubble trails with whistles in this study. Bubble bursts are likely retained from the artiodactyl snort produced in response to startling or dangerous situations. As a result, I anticipated high portions of aggressive or sudden behaviors by bystanders preceding bubble bursts. Additionally, bubble producers may engage in aggressive or flee responses during or following bubble bursts. Scant bubbles are a newly identified behavior; thus, it is unknown what behaviors will be associated with scant bubble emissions, or whether those behaviors will differ across time periods. Due to their small size, I anticipate scant bubbles to be used as a short range communication in affiliative contexts. Alternatively, scant bubbles may be unintentional air release during a period of high engagement. Otherwise, scant bubbles may be minute versions of bubble trails, in which case the behaviors present would match those of bubble trails. Finally, I anticipated females would produce more bubbles than males, and bubble production would vary by age class with the greatest amount of bubbles produced by subadults, followed by juveniles, then adults, and finally calves, and that bubble events will frequently have calves as bystanders, following previous studies (Beard, 2007).

Benefit

This study will greatly improve scientific understanding of bubble use in bottlenose dolphins. By demonstrating differences in presence of behaviors and how they change with the introduction of bubble production for different bubble types, we can more easily identify bubble functions and how they fit into the overall behavioral repertoire of bottlenose dolphins. Furthermore, demographic information provides insight into whether bubble productions are utilized differently by sex or age class. An improved understanding of the function of bubble production types increases accuracy when these behaviors are used in reporting results, rather than relying on the assumed functions which have been perpetuated without empirical support. This provides support for use of bubble behaviors as responses or behavioral variables in experimental and observational studies.

CHAPTER II - METHODS

Population

Study subjects consist of a population of bottlenose dolphins (*Tursiops truncatus*) at the Roatan Institute for Marine Sciences, a component of Anthony's Key Resort in Roatan, Honduras. The dolphins are housed in a sea pen spanning from the shoreline to 8m in depth and covering 300m^2, with a natural sea floor composed of sand, rocks, sea grass, and coral. Individuals in the population are identifiable via a combination of unique permanent features and temporary rake marks. Population size varied between 20 and 30 individuals during the years data were collected. All individuals receive regular human interaction, and are thus habituated to human presence, which minimized potential disturbance from data collection. Additionally, this population is reflective of wild populations with respect to age and sex distribution as well as interaction behaviors (Dudzinski et al., 2012; Dudzinski, Gregg, Paulos, & Kuczaj, 2010), making it an ideal model for behavioral studies.

Data

Data consisted of underwater high definition video collected by S. Kuczaj in January, February, March, and May of 2013 and March of 2014. Recording utilized an opportunistic brief focal follow sampling methodology during times when all individuals were in the enclosure and there was no potential interference from guests or training staff. Raw video totaled 19 hours, 34 minutes, and 57 seconds. From these videos, 2511 bubble production events were identified and isolated for analysis. Bubble production was defined as a dolphin releasing air underwater from the blowhole in a manner resulting in the formation of bubbles. The events were split into time periods of before, during, and after the bubble production occurred. During was defined as while the bubbles were being released from the blowhole, while before and after were defined as the 5 seconds immediately preceding and following the bubble release, respectively.

Table 1

Bubble types.

Bubble Type	*Operational Definition*
Bubble Trail	A series of small bubbles produced from the blowhole that form a trail; pauses between trails must be greater than 1 second to constitute a new bout
Bubble Burst	A sudden release of air from the blowhole resulting in a large cloud of bubbles
Scant Bubbles	Bubbles which are small, sparse, and few

The bubble type of each bubble production event was identified as a bubble burst, bubble trail, or scant bubble (Table 1). Of the bubble events identified, 2189 were bubble trails, 122 were bubble bursts, and 202 were scant bubbles. Due to the disproportionately high number of bubble trails, 250 bubble trail events were randomly selected for analysis. For each individual present during the bubble event, their role as bubble producer or bystander and ID, when possible, was be recorded. Additionally, rates of observed behaviors (Table A1), defined as duration per time period length, were continuously recorded for the before, during, and after time periods for each individual present. As bubble production can occur within the coding window of other instances of bubble production, cases of multiple bubble production events in overlapping time frames were all included as separate events and coded as an observed behavior in the appropriate time period of the other bubble event(s). Reliability between coders was calculated on 20% of the bubble events selected for analyses. Coders were required to have a minimum of 80% agreement on behaviors and identification for data to be included for analyses.

Analysis

As the majority of behaviors were not present in over 90% of cases, behaviors were grouped by function into 11 behavioral categories (Table 2) to ensure sufficient variability was available for analyses. Multiple researchers familiar with dolphin behavior were consulted to construct the categories. Correlation matrices were run to determine if behavioral groupings correlated with one another. The behaviors of take object and exchange were removed because they did not occur in the data; while watch bubbles and interact with bubbles were removed because they only occurred in one instance.

Table 2

Behavioral groupings of coded behaviors.

Behavioral Group	*Behaviors*
Aggression	Bite/Rake, Hit, Head to Head Circling, Push, Ram, Chase, Jaw Clap, Head Jerking / Posturing
Avoidance	Avoid/ Flee, Flinch, Leaping
Object Manipulation	Mouthing, Object Manipulation, Bottom Grubbing, Orient to Object
Sexual	Erection, Goosing, Group social ball, Mounting, Sexual Petting
Contact	Pec rub, Petting, Rubbing, Body Rub, Tactile, Brush Past
Synchronous Swim	Group swim, Pair swim, Pair swim with contact
Surfacing	Breathe, Synchronous Breath
Interest	Head Scanning, Approach, Follow, Orient to Dolphin
Bubble Production	Bubble Trail, Bubble Burst, Scant Bubble
Open Mouth	Open Mouth
Human Interaction	Interact with Human, Orient to Camera, Orient to Person

Logistic regression analyses were used to determine if rates of behavior factors and demographics can be used to predict whether an individual will produce a bubble or simply be present during bubble production. To account for differences in bubble type and time period, a separate logistic regression was run for each bubble type and time period combination, resulting in nine prediction models. Chi-square was used to determine if bubble production frequency differed between males and females. All analyses were conducted in SPSS.

CHAPTER III - RESULTS

Reliability

Reliability between two coders on 20% of bubble events across all sampling periods was achieved for both identification and behavioral coding. Dolphin identification between coders had 94.5% agreement with Cohen's Kappa = 0.762 indicating good agreement. Behavioral coding between coders was well correlated with a Pearson's $r = 0.805$.

Behavioral Predictors by Bubble Type

Behavioral groupings

In all times periods, there were instances of significant correlation between behavioral groupings (Table 3).

Table 3

Correlations between behavioral groupings

Before	*Aggression*	*Avoidance*	*Object Manipulation*	*Sexual*	*Contact*	*Sync Swim*	*Surfacing*	*Interest*	*Bubble*	*Open Mouth*	*Human Interaction*
Aggression		.000	-.013	.003	-.009	-.060**	-.035	.018	.014	.232**	-.020
Avoidance	.000		-.010	.008	-.003	-.046*	-.007	.003	.058**	-.010	-.018
Object Manipulation	-.013	-.010		-.011	-.003	-.039*	.030	.020	.003	.114**	.008
Sexual	.003	.008	-.011		.046*	-.046*	.017	.038*	.070**	.029	-.010
Contact	-.009	-.003	-.003	.046*		.135**	.070**	.043*	.058**	.110**	.028
Sync Swim	-.060**	-.046*	-.039	-.046*	.135**		-.002	-.080**	-.074**	-.117**	.006
Surfacing	-.035	-.007	.030	.017	.070**	-.002		-.008	.034	.028	.060**
Interest	.018	.003	.020	.038*	.043*	-.080**	-.008		.070**	.182**	.060**
Bubble Production	.014	.058**	.003	.070**	.058**	-.074**	.034	.070**		.169**	.085**
Open Mouth	.232**	-.010	.114**	.029	.110**	-.117**	.028	.182**	.139**		.051**
Human Interaction	-.020	-.018	.008	-.010	.028	.006	.060**	.060**	.085**	.051**	

Table 3(continued).

During	***Aggression***	***Avoidance***	***Object Manipulation***	***Sexual***	***Contact***	***Sync Swim***	***Surfacing***	***Interest***	***Bubble***	***Open Mouth***	***Human Interaction***
Aggression		-.006	-.007	.019	-.011	-.053**	-	-.009	-	.196**	-.014
Avoidance	-.006		-.004	-.007	-.009	-.035	-	-.005	-	.021	-.008
Object Manipulation	-.007	-.004		.110**	-.011	-.042*	-	-.006	-	.008	-.010
Sexual	.019	-.007	.110**		.001	-.064**	-	.000	-	.018	-.015
Contact	-.011	-.009	-.011	.001		.084**	-	-.008	-	.011	-.002
Sync Swim	-.053**	-.035	-.042*	-.064**	.084**		-	-.018	-	-.078**	.003
Interest	-.009	-.005	-.006	.000	-.008	-.018	-		-	.016	-.008
Open Mouth	.196**	.021	.008	.018	.011	-.078**	-	.016	-		.072**
Human Interaction	-.014	-.008	-.010	-.015	-.002	.003	-	-.008	-	.072**	

Table 3(continued).

After	***Aggression***	***Avoidance***	***Object Manipulation***	***Sexual***	***Contact***	***Sync Swim***	***Surfacing***	***Interest***	***Bubble***	***Open Mouth***	***Human Interaction***
Aggression		.014	.022	-.015	.033	-.034	-.025	.049*	.049*	.188**	-.010
Avoidance	.014		-.006	-.007	.001	-.023	-.013	-.001	.033	-.009	-.012
Object Manipulation	.022	-.006		.045*	.015	-.040*	.037	-.009	-.009	.095**	.018
Sexual	-.015	-.007	.045*		.068**	-.065**	.107**	-.020	.038	.029	-.012
Contact	.033	.001	.015	.068**		.142**	.045	.021	.046*	.079**	.000
Sync Swim	-.034	-.023	-.040*	.065**	.142**		-.006	-.077**	-.055*	-.093**	-.029
Surfacing	-.025	-.013	.037	.107**	.045*	-.006		.044*	.080**	.040*	.065**
Interest	.049*	-.001	-.009	-.020	.021	-.077**	.044*		.088**	.112**	.018
Bubble Production	.049*	.033	-.009	.038	.046**	-.055**	.080**	.088**		.165**	.048*
Open Mouth	.188**	-.009	.095**	.029	.079**	-.093**	.040*	.112**	.165**		.048*
Human Interaction	-.010	-.012	.018	-.012	.000	-.029	.065**	.018	.048*	.048*	

Note: Significant correlations are indicated with * at the < 0.05 level and with ** at the <0.01 level

Bubble trails

Logistic regression utilizing behavior and demographic variables to predict whether or not an individual was the bubble producer of a bubble trail event successfully generated models for before, during, and after time periods (Table 4). All models significantly improved fit over the naive model $p < .001$. The model for predicting bubble production from behaviors before a bubble trail improved percentage classification from 76.1 to 77.3 percent. The model for predicting bubble production from behaviors during a bubble trail improved percentage classification from 76.2 to 79.1 percent. The model for predicting bubble production from behaviors after a bubble trail improved percentage classification from 76.2 to 77.5. Individuals were more likely to be producers during bubble trail events if they were not calves. Additionally, they were more likely to produce a bubble trail if they exhibited higher rates of interest or open mouth before or during; surfacing or bubble production behaviors preceding or following; higher rates of sexual behavior during; higher rates of synchronous swimming after; or human interaction before, during, or after bubble trails were produced.

Table 4

Logistic regression models for predicting whether an individual is a bubble producer based on demographics and behaviors exhibited before, during, and after bubble trail events.

	Before			During			After		
Predictor	β	P	Odds Ratio	β	P	Odds Ratio	β	P	Odds Ratio
Calf	**-.850**	**<.001**	**.427**	**-.865**	**<.001**	**.421**	**-.802**	**<.001**	**.449**
Male	-.068	.677	.934	-.122	.449	.885	.030	.855	1.030
Aggression	.66	.728	1.934	-.33	.701	.719	.939	.359	2.559
Avoidance	.685	.707	1.984	1.533	.224	4.633	-.557	.788	.573
Object Manipulation	2.417	.107	11.207	1.712	.199	5.541	1.837	.173	6.278
Sexual	.347	.455	1.415	**1.021**	**.039**	**2.776**	.217	.617	1.242
Contact	-.074	.910	.928	.244	.516	1.277	1.155	.102	3.175
Sync Swim	-.199	.329	.820	-.061	.739	.941	**-.493**	**.026**	**.611**
Surfacing	**2.268**	**<.001**	**9.660**	-	-	-	**3.838**	**<.001**	**46.455**
Interest	**2.152**	**.010**	**8.600**	**2.647**	**.001**	**14.117**	1.013	.214	2.753
Bubble Production	**1.609**	**<.001**	**4.997**	-	-	-	**2.016**	**<.001**	**7.507**
Open Mouth	**1.398**	**.007**	**4.047**	**1.526**	**<.001**	**4.6**	.582	.221	1.789
Human Interaction	**4.962**	**<.001**	**142.897**	**3.090**	**<.001**	**21.974**	**3.268**	**.002**	**26.263**
Constant	-1.390	<.001	.249	-1.344	<.001	.261	-1.368	<.001	.255

Note: Significant predictors are bolded

Bubble bursts

Logistic regression utilizing behavior and demographic variables to predict whether or not an individual was the bubble producer of a bubble burst event successfully generated models for before, during, and after time periods (Table 5). All models significantly improved fit over the naive model $p < .001$. The model for predicting bubble production from behaviors before a bubble burst improved percentage classification from 76.6 to 79.9 percent. The model for predicting bubble production from behaviors during a bubble burst improved percentage classification from 76.5 to 77.5 percent. The model for predicting bubble production from behaviors after a bubble burst improved percentage classification from 76.5 to 80.3 percent. Individuals were more likely to be producers during bubble burst events if they were not calves. Individuals were more likely to produce a bubble burst if they exhibited higher rates of object manipulation or bubble production before; human interaction during; surfacing following; or sexual behavior or open mouth before, during, or after bubble bursts were produced. Additionally, a few behaviors were not significant but provide information about how bubble bursts fit into the behavioral repertoire. Avoidance was marginally significant before bubble bursts with 7 out of 10 instances of avoidance exhibited by the bubbler, was not included during bubble bursts despite the only instance being displayed by the bubbler, and was not significant after although all 4 instances were exhibited by the bubble producer. Object manipulation during bubble bursts was also non-significant with one instance exhibited by the bubble producer.

Table 5

Logistic regression models for predicting whether an individual is a bubble producer based on demographics and behaviors exhibited before, during, and after bubble burst events.

	Before			During			After		
Predictor	β	P	Odds Ratio	β	P	Odds Ratio	β	P	Odds Ratio
Calf	**-1.105**	**<.001**	**.331**	**-1.162**	**< .001**	**.313**	**-1.014**	**<.001**	**.363**
Male	.105	.698	1.110	-.055	.821	.946	.210	.453	1.234
Aggression	.954	.438	2.596	-.687	.496	.503	-1.174	.584	.309
Avoidance	*7.906*	*.066*	*2714.075**	-	-	-	110.323	.999	8.176 x10^{47}*
Object Manipulation	**3.011**	**.003**	**20.313**	21.865	1.00	3131554831*	*2.831*	*.086*	*16.967*
Sexual	**1.179**	**.003**	**3.250**	**1.781**	**.004**	**5.935**	**1.247**	**.043**	**3.479**
Contact	.770	.536	2.159	.681	.572	1.975	1.149	.390	3.156
Sync Swim	-.213	.482	.809	-.399	.572	.671	-.088	.799	.916
Surfacing	-1.951	.247	.142	-	-	-	**8.643**	**<.001**	**5670.441**
Interest	-.810	.645	.445	-19.324	1.00	0.000*	.574,	.737	1.775
Bubble Production	**2.412**	**.016**	**11.160**	-	-	-	1.622	.111	5.638
Open Mouth	**2.422**	**.003**	**11.269**	**1.233**	**.023**	**3.431**	**1.622**	**.044**	**5.062**
Human Interaction	2.273	.109	9.710	*1.571*	*.051*	*4.812*	-.263	.896	.769
Constant	**-1.414**	**<.001**	**.243**	-1.259	.997	.284	-1.438	.994	.237

Note. Significant predictors are bolded. Marginally significant predictors are italicized. Additional behaviors of interest are indicated with an asterisk.

Scant bubbles

Logistic regression utilizing behavior and demographic variables to predict whether or not an individual was the bubble producer of a scant bubble event successfully generated models for before, during, and after time periods (Table 6). All models significantly improved fit over the naive model $p < .001$. The model for predicting bubble production from behaviors before a scant bubble improved percentage classification from

72.6 to 75.7 percent. The model for predicting bubble production from behaviors during a scant bubble improved percentage classification from 72.6 to 75.4 percent. The model for predicting bubble production from behaviors after a scant bubble improved percentage classification from 72.6 to 75.0 percent. Individuals were more likely to be producers during scant bubble events if they exhibited higher rates of object manipulation, surfacing, or bubble production before or after; higher rates of open mouth before or during; higher rates of synchronous swim or contact during or after; higher rates of human interaction before, during, or after scant bubbles were produced. Additionally, a few behaviors were not significant but provide information about how scant bubbles fit into the behavioral repertoire. Avoidance was non-significant before bubble production with 3 instances all exhibited by bystanders, non-significant during with one instance exhibited by the bubble producer, and was not present after bubble production. Interest was non-significant during scant bubble production with two instances both exhibited by the bubble producer.

Table 6

Logistic regression models for predicting whether an individual is a bubble producer based on demographics and behaviors exhibited before, during, and after scant bubble events.

	Before			During			After		
Predictor	β	P	Odds Ratio	β	P	Odds Ratio	β	P	Odds Ratio
Calf	-.275	.144	.760	-*.312*	*.081*	*.732*	-*.310*	*.098*	*.733*
Male	-.107	.560	.898	-.114	.517	.892	-.201	.818	.818
Aggression	-2.090	.564	.124	1.083	.447	2.955	2.997	.229	20.027
Avoidance	-98.169	.999	.000*	20.865	1.0	1151903802*	-	-	-
Object Manipulation	**1.833**	**.042**	**6.253**	.472	.523	1.602	**2.130**	**.031**	**8.415**
Sexual	-.525	.465	.592	-.232	.698	.793	-.781	.288	5.686
Contact	.358	.599	1.430	**1.98**	**.010**	**2.997**	**1.738**	**.023**	**5.686**
Sync Swim	-.301	.194	.740	**-.424**	**.031**	**.655**	**-.463**	**.031**	**.629**
Surfacing	**2.836**	**< .001**	**17.042**	-	-	-	**2.784**	**< .001**	**16.189**
Interest	1.094	.202	2.986	22.073	.999	3856597012*	1.417	.164	4.126
Bubble Production	**4.483**	**< .001**	**88.510**	-	-	-	**4.989**	**< .001**	**146.845**
Open Mouth	**1.363**	**.028**	**3.909**	**1.208**	**.001**	**3.348**	.657	.209	1.930
Human Interaction	**5.813**	**< .001**	**334.456**	**2.507**	**< .001**	**12.265**	**4.543**	**< .001**	**93.996**
Constant	-1.405	.997	.245	-.871	.997	.419	**-1.090**	**< .001**	**.336**

Note. Significant predictors are bolded. Marginally significant predictors are italicized. Additional behaviors of interest are indicated with an asterisk.

Sex differences

Chi-square tests for difference in bubble production frequency by sex were not significant for all bubble types [Bubble trails X^2 (1, N = 1005) = .868; Bubble bursts X^2 (1, N = 463) = .046; Scant bubble X^2 (1, N = 730) = .448].

CHAPTER IV — DISCUSSION

Summary

A few overarching trends emerged in the behaviors which predict production of each of the three bubble types. Respiration is closely linked to bubble production, as are behaviors indicative of increased arousal levels in various contexts. Additionally, each bubble type appears to have multiple uses as the behaviors predicting the production of each type do not cohesively describe a single context or function. Instead, it is more likely that bubble productions are signals which are modified by concurrent behaviors and are thus flexible in usage, allowing the animal to convey information in a range of situations.

An individual surfacing after bubble production for all bubble types, or before bubble production for bubble trails and scant bubbles, is more likely to be a bubble producer. Previous reports of respiration rates in adults demonstrate the typical inter-breath interval of adult bottlenose dolphins to vary between 16 and 50 seconds (Fahlman et al., 2016; Mann & Smuts, 1999; McCormick, 1969), indicating dolphins could have easily spent the entire sampling period for each bubble event without respiration. While some respiration is likely to fall in proximity to bubble emissions purely from chance, the increased likelihood of an animal being a bubble producer if engaging in surfacing behavior indicates they are either increasing respiration rates, timing their respiration and bubble emission to occur in proximity, or engaging in another behavior which requires surfacing. This increase in surfacing behavior for bubble producers of all bubble types suggests bubbles require the loss of a valuable resource which must be quickly replenished. Additionally, calves may be more subject to stress on respiration from bubble production, as infants breathe more frequently (Mann & Smuts, 1999) and their blood oxygen storage cell concentrations do not reach adult levels until 3 years of age (Noren, Lacave, Wells, & Williams, 2002). However, it is important to note dolphins can be at the surface without engaging in respiration, so while respiration requires surfacing, surfacing does not automatically entail respiration.

Behaviors which were not observed can provide insights into the functions of bubble productions as well. While object manipulation was observed in conjunction with bubble production, neither object exchange nor take object were observed in the events selected for analysis. This was likely due to a sparsity of events in these categories occurring during the sampling period. Both object exchange and take object were coded due to their observation in previous behavioral research with this population (Moreno, Highfill, & Kuczaj, 2017); however, they occurred relatively rarely and most instances were in May of 2014, which was not included in the present study.

Of greater interest, only one instance of bubble engagement was observed, despite the prevalence of bubble play reported in the literature. There are two potential explanations for this. First, bubble play may be socially transmitted (Jones & Kuczaj, 2014), and these individuals typically do not have social contact with dolphins from other populations, unlike dolphins in many facilities in the US which have opportunities to interact with dolphins from other populations during breeding programs or may move facilities during their lifetime. The other is that with the rich social and physical environment they inhabit, there may be too much else occupying these individuals for bubbles to be of much interest. These individuals are frequently observed playing with objects in their environment such as seaweed and seashells (Greene, Melillo-Sweeting, & Dudzinski, 2011), and likely do not find bubbles to be as rewarding of a toy. In conjunction with these reasons, bubble play may be overrepresented in the literature due to human interest generating numerous reports on a relatively infrequent behavior. Similarly, bubble rings may not have been observed due to a lack of opportunity for social learning of the behavior and little interest in producing ephemeral objects for manipulation. This lack of bubble production for the sake of engaging with the bubbles themselves further supports the conclusion that bottlenose dolphins use bubbles as a communicative signal.

While the results presented here are useful in empirically investigating the usage of bubble bursts, bubble trails, and scant bubbles in bottlenose dolphins, there are limits to the conclusions which can be drawn from the present study. Due to the large numbers of behaviors originally included in behavioral coding and the relative infrequency of the majority of those behaviors, available analyses were limited and behaviors had to be consolidated into behavioral groupings based on previous understanding of functionality. Some of these behavioral groupings were weakly correlated during each of the three time periods, which may have influenced the findings presented here. Additionally, the exploratory nature of this investigation limited our ability to look at details in usage of each bubble type or to focus on highly specific aspects of bubble usage. However, these results provide preliminary results on which further, more detailed studies can expand.

Bubble Trails

Demographic findings of bubble trail producers and non-producers had both similarities and differences with previous literature. Matching previous findings (Beard, 2007), calves were significantly more likely to not be bubble producers, indicating they are present during bubble production events more than they are focal bubble producers. Calf presence indicates they may be playing a key role in eliciting elicit bubble production by other animals. This suggests future studies should investigate whether particular calf behaviors increase bubble trail production in other individuals. Contrary to previous reports (Beard, 2007), no difference in bubble production was found between sexes. This may be due to a difference in methodology or between populations. Additionally, while males and females both use bubble trails, it is unknown whether both sexes utilize them in the same manner or situations. This could be determined through examining if there is an interaction between behavioral utilization of bubble trails and the sex of the individuals involved.

Bubble trails are clearly used in relation to a number of social situations, including investigation, synchronous swimming, and sexual interactions. Together, the increased probability that an individual engaging in interest, open mouth, or human interaction behaviors is the individual producing a bubble trail indicate this bubble type is congruent with engagement that is likely social, investigative, or both. Moreover, interest and open mouth were no longer predictors following emission of the bubble trail, most likely due to cessation of bubble production concurrent with a change in focus by the bubble producer.

Additional evidence for a social role for bubble trails is the greater probability of individuals engaging in synchronous swim being non-bubble producers after bubble production. Initially, this seems counter intuitive, as it may indicate bubble producers are engaging in less synchronous behavior following bubble trails. However, the nature of synchronous swimming requires the involvement of a minimum of one individual not producing a bubble for every individual involved which is a bubble producer. Thus, an increase in synchronous behavior of other animals may be from those animals joining the bubble producer rather than the bubble producer leaving synchrony. Unfortunately, this difference cannot be determined from current results. Future research should quantify whether synchronous behavior of bubble producing animals increases, decreases, or is unchanged with production of bubble trails, and whether the bubble trail elicits an increase in synchronous behavior from other individuals towards the bubble producer. Better understanding signals involved in synchronous behavior is of particular importance for bottlenose dolphins as synchrony plays an important role in male-male alliances (Connor, Smolker, & Bejder, 2006; Connor, Wells, Mann, & Read, 2000) and mother-calf relationships (Fellner, Bauer, Stamper, Losch, & Dahood, 2013; Mann & Smuts, 1999). Considering these relationships, future research should also investigate if sex or relatedness changes how bubble trails are used in relation to synchronous swimming behavior.

The third social situation bubble trails are related to is that of sexual interactions, which are an important component of social bonding (Botero Acosta, 2015; Harvey, Dudzinski, & Kuczaj, 2017; Mann, 2006; Moreno et al., 2017). During, but not preceding or following, bubble trail production individuals had an increased likelihood of being the producer when exhibiting sexual behavior. This could provide additional information about the sexual interaction to the recipient or other animals in proximity. Alternatively, this could indicate individuals are likely to not produce bubbles while a recipient of sexual behavior, perhaps to conserve air. In either case, sexual behavior before and after bubble trails does not significantly predict whether an individual is a bubble producer or not, indicating sexual behavior is similar for producers and non-producers during these time periods. This finding indicates further research on the role of bubble trails during sexual behavior is needed.

Previous literature has indicated that bubble trails are observed in conjunction with aggressive behaviors in spotted dolphins (Dudzinski, 1998). While some aggressive and avoidance behaviors were seen, these were not significantly different between bubble producers and bystanders. Thus, from the present results, the role of bubble trails in aggressive encounters is inconclusive, and further studies needed to examine whether bubble trails are linked with aggressive behavior in bottlenose dolphins.

Consistent with previous literature (Beard, 2007), bubble trail events were often linked to other bubble productions by the bubble producer. This indicates multiple bubble events were used in conjunction with one another, and thus repeated use of bubbles, sometimes of differing types, may provide additional information to nearby animals and serve as a more beneficial signal than single bubble productions. Beard (2007) also found an increase in bubble trails in response to bubble trails produced by other individuals. Current results do not exclude the possibility of other individuals also producing bubbles, however they do not support the hypothesis of bubble trails functioning as responses to other bubble trails. Future research is needed to better understand the relationship of bubble trail production to other bubble trails.

Finally, the existence of a relationship between bubble trails and behaviors indicates whistles produced in conjunction with bubble trails are likely not representative of the whistle repertoire. While this agrees with one perspective on the whistle trail debate (Fripp, 2005, 2006), this is not definitive and requires further research. To understand the relationship between bubble trails and whistle production, an incorporation of whistles would be needed and was not possible with this data set due to the quantity of individuals and a lack of localization equipment.

Bubble Bursts

Similar to bubble trails, calves were more likely to be present than producers in conjunction with bubble burst events. This may be due to increased usage of bubble bursts in response to calf presence, or greater use of bubble bursts by more mature individuals. Examining the behaviors of calves associated with bubble bursts which may elicit their production by other individuals and the proportion of bubble burst events produced by each age group could be used to differentiate between these possibilities.

Behavioral predictors of which individual produced a bubble burst generally supports previous findings of bubble bursts as signals used in aggressive, and high interest or engagement situations. Although bubble bursts were predicted to also indicate surprise or a startle response, this hypothesis is not supported from the present results. This is likely due to a lack of surprising events occurring in the study. The most robust evidence indicative of bubble bursts as indicators of interest or engagement come from the increased likelihood an individual is producing the bubble if engaging in object manipulation. This manipulation was most likely object play, an important developmental behavior for bottlenose dolphins (Cappiello, 2017; Greene et al., 2011). Thus, it would be reasonable to expect individuals engaged in object play to be cognitively invested in their actions.

Two additional behavior groupings which predicted bubble production could be interpreted as indicative or either aggressive or interest situations. These behavioral groups are human interaction and open mouth. Human interaction included orienting to humans or the camera and tactile interaction with a human. These could be interpreted as social or investigative situations. Additionally, orient to camera was the most common of the behaviors in this category, thus dolphins may have been interacting with their reflection. As dolphins may (Reiss & Marino, 2001) or may not (Loth, von Fersen, Gunturkun, & Janik, 2015) be able to identify themselves in a reflective surface, it is difficult to determine the type of interaction occurring with the camera or the function of the bubble bursts produced during that interaction. Possibilities include and are not limited to: interest, surprise, motor play, threat, and response to perceived threat. Open mouth behavior likely has multiple functions (Kuczaj & Frick, 2015), and thus could have been in an aggressive context as a display or could have been engagement with an object in conjunction with object manipulation. Both potential uses support findings from other functional behavioral groups regarding the usage of bubble bursts.

Although avoidance behavior occurred relatively rarely for all bubble types, there appears to be a link between these behaviors and bubble burst production. This establishes bubble bursts as part of a suite of avoidance or fear response behaviors, consistent with previous predictions. However, it would be expected that a behavior linked to reactionary behaviors would also have increased levels of aggression in other individuals, particularly those behaviors directed at the bubble producing animal. The most likely explanation for the lack of significance in aggression as a predictor in the current study is that the bubble producer and other individuals present all engaged in aggressive behaviors. This hypothesis would be supported if elevated levels of aggression either by or directed at the bubble producer are linked to bubble burst production. Additionally, little is currently known about the exact role which bubble bursts play in aggressive encounters. While present findings suggest bubble bursts are most likely a response coupled with avoidance behavior, this does not exclude the possibility they may be used as a threat display or to settle disputes before more costly escalation occurs. Future research can begin to differentiate between these uses by determining if conflict is more likely to increase or decrease following bubble burst production.

Production of bubbles before a bubble burst predicts the individual is more likely to be the producer of the focal bubble burst as well. This indicates bursts are used in conjunction with other bubbles, which may convey additional information or be used as an initial signal. As bubble bursts release more air in a shorter time than other bubble types, this could be an effort to conserve resources through use of a less costly signal first. As escalation of signals is a common feature of interindividual conflict (Archer &

Huntingford, 1994), this supports the hypothesis of bubble bursts as a display in aggressive situations. However, as the bubble types used before bubble bursts are not differentiated and the relationship between bubble bursts and aggressive behavior remains uncertain, more evidence is needed to support this conclusion.

Sexual behavior at all time points predicted bubble burst production, a result which was not anticipated from previous literature on bottlenose dolphins. Bubble bursts have been observed as part of courtship behavior in spotted dolphins (Herzing, 1996), and may be similarly used by bottlenose dolphins in sexual situations. As bubble burst production incurs some cost on respiration due to the large volume of air lost, bubble bursts may be indicative of respiratory fitness and advertise mate quality through the handicap principle (Grafen, 1990; Zahavi, 1975). It is also important to note that the vast majority of sexual behavior observed in this population is male-male (Botero Acosta, 2015), and thus the sexual behavior observed with bubble bursts was primarily non-reproductive in nature. As a result, bubble bursts concurrent with male-male sexual behavior may serve as practice for later use with females, display for nearby females, or part of the sexual behavioral repertoire that is commonly produced in any type of sexual situation.

Alternatively, sexual behavior in bottlenose dolphins is typically very active and may also involve high energy affiliative or aggressive behaviors. Thus, the bubble bursts produced here may be indicative of high arousal levels rather than specifically linked to sexual behaviors. Further examination of the role of bubble bursts both during sexual behavior and generally will be needed to determine which is the more likely cause.

Whether bubble bursts are indicative of reproductive fitness could be determined by whether males which produce larger or more frequent bubble bursts have more robust respiratory systems, are healthier, or have more offspring. Additionally, an examination of bubble production specific to sexual interactions would be useful in determining how the usage of bubble bursts during sexual behavior differs from that of bubble trails, which these results have also demonstrated to be linked to sexual behavior.

Surfacing behavior was slightly different for bubble bursts than other bubble types. The increase in surfacing behavior following, but not preceding bubble bursts is likely due to two factors. First, bubble bursts involve a loss of a large quantity of air, which would need to be replenished. Second, some bubble bursts were clearly early exhalation; these events consisted of an animal which released a large quantity of air while still underwater, and then immediately broke the surface. Exhaling while still underwater would be more efficient, as it would allow the animal to remove old air before breaking the surface. This would decrease the time spent at the surface for gas exchange, minimizing swimming under higher drag conditions (Fish & Rohr, 1999) and away from the animal's present activity. This would be especially important if the individual was actively involved in another time, attention, or physiologically demanding behavior. As bubble bursts are likely to occur in conjunction with interest, avoidance, aggressive, or sexual behaviors, they may also be associated with a greater need for quick respiration to minimize time and energy expenditure.

Scant Bubbles

Consistent with other bubble types, scant bubbles exhibit a clear link between bubble production and respiration. Given the low volume of air released during a scant bubble, it is highly unlikely the bubble producer would physiologically need to surface to replenish air. One possibility for the proximity with surfacing is that the dolphin is adjusting the amount of air in its lungs. Another is that as the scant bubble producer is also likely to produce other bubbles, this would result in greater air loss than just production of the scant bubble alone, which would put additional strain on oxygen needs and may be the prompt for additional surfacing. This hypothesis could be tested by determining if the bubble producer in events in which additional bubbles are produced surfaces more than in events which do not have additional bubbles produced.

The behavioral predictors of scant bubble production exhibit many similarities with bubble trails. This indicates scant bubbles may be functionally equivalent to bubble trails, with their main difference being size. However, due to slight differences in behaviors which predict production of each bubble type, it is more likely that the scant bubble is a variation of the bubble trail.

The first clear similarity between bubble trails and bubble bursts is the increased likelihood of an individual not being a bubble producer if engaging in synchronous swimming. As explained for bubble trails, this could be due to either the bubble production bringing in more non-bubble producing animals or due to the focal bubble producer leaving synchronicity. In addition, an increased likelihood of an individual producing a scant bubble if engaging in contact, an important social behavior for dolphins

(Dudzinski et al., 2010; Kaplan & Connor, 2007; Sakai, Hishii, Takeda, & Kohshima, 2006; Tamaki, Morisaka, & Taki, 2006), during or after bubble production further supports the link with social behavior and suggests scant bubbles may be used in close-proximity situations where bubble trails are not. Together, synchronous swimming exhibited by individuals not producing bubbles and contact behavior by the individual producing a bubble indicates the scant bubble likely plays a role in changing social engagement between individuals.

Also resembling bubble trails, scant bubble producers exhibit multiple behaviors indicative of engagement and increased arousal levels. These behaviors are human interaction, object manipulation, and open mouth, which together indicate this other use of scant bubbles is likely primarily non-social. The exceptions to note here are that open mouth could be social or not social depending on what it is directed at and interact with human behaviors would have included both non-social behaviors such as orient to camera and social behaviors such as interact with human. However, the nature of social interaction with a member of a different species is likely to differ from intraspecies interactions. This elicits the question of why produce bubbles at all, if there is not a communicative or physical function to the bubbles. I suspect these emissions are unintentional, likely because the animal is so absorbed by an object of interest that it leaks a small amount of air, similar to how an overly excited dog might leak a small quantity of urine.

Finally, it is worth noting the rarity of avoidance behavior exhibited at any time period associated with a scant bubble. This indicates scant bubbles are not part of a fear or flee response. Instead, they occur in non-threating situations of social interaction or object investigation. Further research on scant bubbles, particularly from additional populations, are needed to confirm this understanding of scant bubble use.

Conclusions

Reports of bubble production by bottlenose dolphins and other cetaceans are peppered though the literature, yet few provide details beyond observation of occurrence or author assessment of the behavioral function. The present study provides a first empirical effort to determine how bottlenose dolphins use three distinct bubble types. Through differences between behaviors of bubble producers and non-producers, it enables a better understanding of how each bubble type fits into the broader behavioral repertoire. Additionally, this study includes the first report of the scant bubble type, which was likely previously unknown due to the difficulty of detection in most observational situations.

These results have identified multiple important points regarding bottlenose dolphin bubble usage. First, all bubble types are used in multiple situations and likely serve as multifunctional signals, which are an important part of the behavioral repertoire. Secondly, bubble productions occur in proximity to one another, indicating signals which work in conjunction to convey additional information. Third, bubble productions occur near surfacing, likely due to their use of respiratory resources. Finally, there are both differences and similarities in how each bubble type is used. Bubble trails are primarily used in social situations such as investigative, synchronous swimming, and sexual behaviors. Bubble bursts occur in conjunction with avoidance, and possibly aggression, behaviors; engagement with objects; sexual behavior; and immediately before surfacing, likely as part of the respiration cycle. Scant bubbles accompany close proximity social behavior and non-social interest, and are not associated with aggression or avoidance situations.

Despite the wealth of findings presented here, bubble production remains a poorly understood behavior and there are numerous gaps to fill in our understanding of their function in bottlenose dolphins. Thus, more research is needed to determine the exact functions of each bubble type and their relationship with other behaviors. Present findings can provide a foundation upon which to build future research, and indicate directions for investigation. Most importantly, future research will benefit from examining bubble use in different contexts separately, as their demonstrated flexibility indicates bubbles will likely group with different behaviors in different situations.

APPENDIX A – Behaviors

Table A1.

Observed Behaviors.

Behavior	*Operational Definition*
Approach	One dolphin approaches another
Avoid/ Flee	Abrupt, rapid, and immediate departure in response to action of another dolphin: often leads into a chase
Bite/rake	Dolphin closes mouth with force around another dolphin, or rubs or slides its open jaw along another with teeth in contact.
Body Rub	Dolphin moves its body along another dolphin in a back and forth motion
Bottom grubbing	Inverted vertically; dolphin rostrum near seafloor and entire body is rotating
Breathe	Dolphin surfaces with blowhole out of the water
Brush Past	Dolphin quickly and forcefully swims past another while in contact
Chase	Rapid and persistent pursuit of another dolphin
Erection	Dolphin has penile erection
Exchange	One dolphin gives something to another such as fish, seaweed, or other object
Follow	One animal follows behind another more than one body length
Goosing	Actor inspects the genital area of the recipient with its rostrum.
Group social ball	Three or more dolphins swim around each other and appear to be "wrestling", such that it is extremely difficult to identify the individual behaviors in which each animal is engaged
Group swim	Three or more dolphins are swimming in same direction within a (dolphin) body length of each other. ~1.5 meters
Head Scanning	Moving head laterally side to side (often while echolocating)
Head to Head Circling	Two dolphins positioned head to head, circling around one another
Head Jerking/ Posturing	Dolphin quickly and forcefully moves head vertically or exhibits an S-posture
Hit	One dolphin contacts another using rostrum or fluke in a quick and aggressive manner
Interact with Bubble(s)	Dolphin interacts physically with bubble or bubbles
Jaw clap	Loud popping sound coupled with a fast open and close of mouth
Leaping	Jumps out of water and reenters head first
Mounting	One dolphin's genital area is thrust onto another dolphin's genital area or other body part

Table A1 (continued).

Behavior	*Operational Definition*
Mouthing	Dolphin has object in mouth and is manipulating it but not biting down. Usually occurs with sea grass, ect.
Object Manipulation	Dolphin actively interacts with an object using its rostrum, pec fin, fluke, or another body part, but the object is not in its mouth
Open mouth	Dolphin opens mouth widely, exposing teeth, usually in orientation to a swimmer or another dolphin
Orient to camera	Dolphin turns head to face camera as it passes by
Orient to dolphin	Dolphin turns head towards another dolphin as it passes by
Orient to object	Dolphin turns head towards an object as it passes by
Orient to person	Dolphin turns head towards a person as it passes by
Pair swim	Dolphin is swimming in same direction with another that is within a (dolphin) body length. ≈1.5 meters
Pair swim with contact	Dolphins engage in a pair swim while maintaining contact with one another
Pec rub	One dolphin actively rubs another's body with its pectoral fin
Petting	Pectoral fin to pectoral fin rubbing where active movement between pec fins is observed
Push	Dolphin applies force to another so as to move the recipient
Ram	One dolphin hits another's body with its body at fast speed
Rubbing	A rubbing event where a body part other than the pec fin is used to rub against another dolphin
Sexual Petting	Actor touches the genital area of the recipient with its pectoral fins.
Synchronous Breath	Two or more dolphins surfacing to breathe at the same time
Tactile	When dolphin briefly contacts (touches) another dolphin, person, or object.
Take Object	Dolphin forcefully removes object from the possession of another
Watch Bubble(s)	Dolphin visually follows the bubble or bubbles

Note: Adapted from: Dudzinski, 1996; Frick, 2016; Moreno et al., 2017.

APPENDIX B – IACUC Approval Letter

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.4063 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**14100901**
PROJECT TITLE:	**"Bottlenose dolphin (Tursiops truncates underwater behavior"**
PROPOSED PROJECT DATES:	**10/2014-9/2017**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**Stan Kuczaj**
DEPARTMENT:	**Psychology**
FUNDING AGENCY/SPONSOR:	na
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2017**

[signature] _____October 9, 2014_____________

Frank Moore, Ph.D. Date
IACUC Chair

REFERENCES

Ames, A. E. (2016). *Pre- and post-partum whistle prodcution of a bottlenose dolphin (Tursiops truncatus) mother-calf dyad* (Master's Thesis). University of Southern Mississippi. Retrieved from http://aquila.usm.edu/masters_theses

Archer, J., & Huntingford, F. (1994). Game theory models and escalation of animal fights. In M. Potegal & J. F. Knutson (Eds.), *The dynamics of aggression: Biological and social processes in dyads and groups* (pp. 3–31). Hillsdale NJ: Lawrence Erlbaum Associates.

Beard, K. L. (2007). *Use of bubble emissions by bottlenose (Tursiops truncatus) and Atlantic spotted dolphins (Stenella frontallis) relative to age and sex* (Master's Thesis). Universtity of Connecticut.

Boisserie, J. R., Fisher, R. E., Lihoreau, F., & Weston, E. M. (2011). Evolving between land and water: Key questions on the emergence and history of the hippopotamidae (*hippopotamoidea, cetancodonta, cetartiodactyla*). *Biological Reviews*, *86*(3), 601–625. https://doi.org/10.1111/j.1469-185X.2010.00162.x

Boness, D. J., Bowen, W. D., Buhleier, B. M., & Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology*, *61*(1), 119–130. https://doi.org/10.1007/s00265-006-0242-9

Botero Acosta, N. (2015). *Same-sex socio-sexual interactions among a group of captive bottlenose dolphins (Tursiops truncatus)* (Master's Thesis). University of Southern Missisippi. Retrieved from http://aquila.usm.edu/masters_theses

Bowles, A. E., & Anderson, R. C. (2012). Behavioral responses and habituation of pinnipeds and small cetaceans to novel objects and simulated fishing gear with and without a pinger. *Aquatic Mammals*, *38*(2), 161–168. https://doi.org/10.1578/AM.38.2.2012.161

Cap, H., Deleporte, P., Joachim, J., & Reby, D. (2008). Male vocal behavior and phylogeny in deer. *Cladistics*, *24*(6), 917–931. https://doi.org/10.1111/j.1096-0031.2008.00223.x

Cappiello, B. M. (2017). *Solitary and Social Object Play in the Bottlenose Dolphin (Tursiops truncatus)*. (Master's Thesis) University of Southern Mississippi. Retrieved from http://aquila.usm.edu/masters_theses

Caro, T., Beeman, K., Stankowich, T., & Whitehead, H. (2011). The functional significance of colouration in cetaceans. *Evolutionary Ecology*, *25*(6), 1231–1245. https://doi.org/10.1007/s10682-011-9479-5

Caro, T. M., Graham, C. M., Stoner, C. J., & Vargas, J. K. (2004). Adaptive significance of antipredator behaviour in artiodactyls. *Animal Behaviour*, *67*(2), 205–228. https://doi.org/10.1016/j.anbehav.2002.12.007

Clark, F. E., Davies, S. L., Madigan, A. W., Warner, A. J., & Kuczaj, S. A. (2013). Cognitive enrichment for bottlenose dolphins (*Tursiops truncatus*): evaluation of a novel underwater maze device. *Zoo Biology*, *32*(6), 608–19. https://doi.org/10.1002/zoo.21096

Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal*

Behaviour, *72*, 1371–1378. https://doi.org/10.1016/j.anbehav.2006.03.014

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social Relationships in a Fission-Fusion Society. In J. Mann (Ed.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago, IL: University of Chicago Press.

Delfour, F., & Aulagnier, S. (1997). Bubbleblow in beluga whales (*Delphinapterus leucas*): a play activity? *Behavioural Processes*, *40*(2), 183–6.

Delfour, F., & Marten, K. (2001). Mirror image processing in three marine mammal species: Killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*) and California sea lions (*Zalophus californianus*). *Behavioural Processes*, *53*(3), 181–190. https://doi.org/10.1016/S0376-6357(01)00134-6

Dudzinski, K. M. (1996). *Communication and behavior in the Atlantic spotted dolphins (Stenella frontalis): relationship between vocal and behavioral activities* (Doctoral Dissertation). Texas A&M University.

Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, *24*(3), 129–142.

Dudzinski, K. M., Gregg, J. D., Paulos, R. D., & Kuczaj, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. *Behavioural Processes*, *84*(2), 559–567. https://doi.org/10.1016/j.beproc.2010.02.013

Dudzinski, K. M., Gregg, J., Melillo-Sweeting, K., Seay, B., Levengood, A., & Kuczaj, S. A. II (2012). Tactile contact exchanges between dolphins: self-rubbing versus inter-individual contact in three species from three geographies. *International Journal of*

Comparative Psychology, *25*, 21–43.

Fahlman, A., van der Hoop, J., Moore, M. J., Levine, G., Rocho-Levine, J., & Brodsky, M. (2016). Estimating energetics in cetaceans from respiratory frequency: why we need to understand physiology. *Biology Open*, *5*(4), 436–442. https://doi.org/10.1242/bio.017251

Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *29*(3). https://doi.org/10.1111/j.1748-7692.2012.00609.x

Fertl, D., & Wilson, B. (1997). Bubble use during prey capture by a lone bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals, 23*(2), 113–114.

Fertl, D., & Würsig, B. (1995). Coordinated feeding by Atlantic spotted dolphins in the Gulf of Mexico. *Aquatic Mammals*, *21*(1), 3–5.

Fish, F. E., & Rohr, J. J. (1999). Review of Dolphin Hydrodynamics and Swimming Performance. (No. SPAWAR/CA-TR-1801). Space and naval warfare systems command. San Diego CA.

Frick, E. E. (2016). *Establishing a link between personality ad social rank in a group of bottlenose dolphins (Tursiops truncatus)* (Master's Thesis). University of Southern Mississippi. Retrieved from http://aquila.usm.edu/masters_theses

Fripp, D. (2005). Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, *21*(1), 29–44.

Fripp, D. (2006). Bubblestream Whistles Are Not Representative of Bottlenose Dolphin

Whistle Repertoires Reply To Mccowan. *Marine Mammal Science*, *22*(2), 496–501. https://doi.org/10.1111/j.1748-7692.2006.00028.x

Gatesy, J., & O'Leary, M. A. (2001). Deciphering whale origins with molecules and fossils. *Trends in Ecology and Evolution*, *16*(10), 562–570. https://doi.org/10.1016/S0169-5347(01)02236-4

Gewalt, W. (1989). Orinoco-freshwater-dolphns (Inia geoffrensis) using self-produced air bubble "rings" as toys. *Aquatic Mammals*, *15*(2), 73–79.

Gnone, G., & Moriconi, T. (2009). Use and function of distinctive whistle-like signals in bottlenose dolphin (*Tursiops truncatus*) mother-calf pair, 1–19.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*(4), 517–546. https://doi.org/10.1016/S0022-5193(05)80088-8

Graur, D., & Higgins, D. G. (1994). Molecular Evidence for the Inclusion of Cetaceans within the Order Artiodactyla. *Molecular Biology and Evolution*, *11*(3), 357–364.

Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing objet play in captive and wild dolphins. *Berkeley Planning Journal*, *24*(1), 292–306. https://doi.org/10.5811/westjem.2011.5.6700

Hain, J. H. W., Carter, G. R., Kraus, S. D., Mayo, C. A., & Winn, H. E. (1981). Feeding behavior of the humpback whale, Megaptera novaeangliae, in the western North Atlantic. *Fishery Bulletin*, *80*(January), 259–268.

Harvey, B. S., Dudzinski, K. M., & Kuczaj, S. A. (2017). Associations and the role of affiliative, agonistic, and socio-sexual behaviors among common bottlenose dolphins (*Tursiops truncatus*). *Behavioural Processes*, *135*, 145–156.

https://doi.org/10.1016/j.beproc.2016.12.013

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins , Stenella frontalis and bottlenose dolphins , *Tursiops truncatus*, 61–79.

Herzing, D. L. (2000). Acoustics and Social Behavior of Wild Dolphins: Implications for a Sound Society. In *Hearing by whales and dolphins* (pp. 225-272). New York, NY: Springer

Hill, H. M. (2009). The behavioral development of two beluga calves during the first year of life. *International Journal of Comparative Psychology*, *22*(4).

Hill, H. M. M., Kahn, M. S., Brilliott, L. J., Roberts, B. M., Gutierrez, C., & Artz, S. (2011). Beluga (*Delphinapterus leucas*) bubble bursts: surprise, protection, or play?, *24*(2).

Jones, B. L., & Kuczaj, S. A. II (2014). Beluga (*Delphinapterus leucas)* Novel Bubble Helix Play Behavior. *Animal Behavior and Cognition*, *2*(2), 206. https://doi.org/10.12966/abc.05.10.2014

Kaplan, J. D., & Connor, R. C. (2007). a Preliminary Examination of Sex Differences in Tactile Interactions Among Juvenile Atlantic Spotted Dolphins (*Stenella frontalis*). *Marine Mammal Science*, *23*(4), 943–953. https://doi.org/10.1111/j.1748-7692.2007.00142.x

Kiley, M. (1972). The vocalizations of ungulates, their causation and function. *Zeitschrift Für Tierpsychologie*, *31*(2), 171–222. https://doi.org/10.1111/j.1439-0310.1972.tb01764.x

Kuczaj, S. A., Frick, E. E., Jones, B. L., Lea, J. S. E., Beecham, D., & Schnöller, F. (2015).

Underwater observations of dolphin reactions to a distressed conspecific. *Learning & Behavior*, *43*, 289–300. https://doi.org/10.3758/s13420-015-0179-9

Kuczaj, S. A. II, & Frick, E. E. (2015). What do dolphins mean when they open their mouths? In *Poster session presented at the meeting for the Society for Marine Mammology*. San Francisco, CA.

Leiner, L., & Fendt, M. (2011). Behavioural fear and heart rate responses of horses after exposure to novel objects: Effects of habituation. *Applied Animal Behaviour Science*, *131*(3–4), 104–109. https://doi.org/10.1016/j.applanim.2011.02.004

Lilley, M. K. (2017). *Sparking a Dolphin's Curiosity: Individual Differences in Dolphins' Reactions to Surprising and Expectation-Violating Events*. University of Southern Mississippi. Retrieved from http://aquila.usm.edu/masters_theses

Loth, A., von Fersen, L., Gunturkun, O., & Janik, V. (2015). Do bottlenose dolphins recognise themselves in a mirror? In *Poster session presented at the meeting for the Society for Marine Mammology*. San Fancisco, CA.

Lusseau, D. (2006). Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops sp.*) in Doubtful Sound, New Zealand. *Behavioural Processes*, *73*(3), 257–65. https://doi.org/10.1016/j.beproc.2006.06.006

Mackay, R. S., & Liaw, H. M. (1981). Dolphin Vocalization Mechanisms. *American Association for the Advancement of Science*, *212*(4495), 676–678.

Mann, J. (2006). Establishing trust: socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In *Homosexual Behaviour in Animals*.

Mann, J., & Smuts, B. (1999). Behavioral Development in Wild Bottlenose Dolphin Newborns (*Tursiops Sp*.). *Behaviour*, *136*(5), 529–566. https://doi.org/10.1163/156853999501469

Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996). Ring bubbles of dolphins. *Scientific American*, *275*(2), 82–7.

McBride, A. F., & Kritzler, H. (1951). Observations on Pregnancy, Parturition, and Postnatal Behavior in the Bottlenose Dolphin. *Journal of Mammalogy*, *32*(3), 251–266. https://doi.org/10.1644/870.1.Key

McCormick, J. G. (1969). Relationship of sleep, respiration, and anesthesia in the porpoise: a preliminary report. *Proceedings of the National Academy of Sciences (USA)*, *62*(3), 697–703.

McCowan, B. (2006). Are Bubblestream Whistles Unrepresentative of Bottlenose Dolphin Whistle Repertoires? *Marine Mammal Science*, *22*(2), 492–495. https://doi.org/10.1111/j.1748-7692.2006.00029.x

McCowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): implications for cognition. *Journal of Comparative Psychology*, *114*(1), 98–106. https://doi.org/10.1037//0735-7036.114.I.98

McCowan, B., & Reiss, D. (1995). Quantitative Comparison of Whistle Repertoires from Captive Adult bottlenose Dolphins (Delphinidae, *Tursiops truncatus*): A Re-evaluation of the Signature Whistle Hypothesis. *Ethology*, (100), 194–209.

McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottle-nosed dolphins (*Tursiops truncatus*): role of learning. *Journal of Comparative Psychology*, *109*(3), 242–260. https://doi.org/10.1037/0735-7036.109.3.242

Merdsoy, B. R., Curtsinger, W. R., & Renouf, D. (2010). American Society of Mammalogists Preliminary Underwater Observations of the Breeding Behavior of the Harp Seal (*Pagophilus groenlandicus*), *59*(1), 181–185.

Moreno, K. R., Highfill, L. E., & Kuczaj, S. A. II (2017). Does personality similarity in bottlenose dolphin pairs influence dyadic bond characteristics? *International Journal of Comparative Psychology*, (30). https://doi.org/10.5811/westjem.2011.5.6700

Noren, S. R., Lacave, G., Wells, R. S., & Williams, T. M. (2002). The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): implications for diving capacity. *Journal of Zoology London*, *258*(1), 105–113. https://doi.org/10.1017/S0952836902001243

O'Leary, M. A., & Gatesy, J. (2008). Impact of increased character sampling on the phylogeny of Cetartiodactyla (Mammalia): Combined analysis including fossils. *Cladistics*, *24*(4), 397–442. https://doi.org/10.1111/j.1096-0031.2007.00187.x

Pace, D. S. (2000). Fluke-made bubble rings as toys in bottlenose dolphin calves (*Tursiops truncatus*), *Aquatic Mammals,* 26(1), 57–64.

Paulos, R. D., Trone, M., & Kuczaj, S. A. (2010). Play in Wild and Captive Cetaceans. *International Journal of Comparative Psychology*, *23*(4), 701–722.

Pryor, K. W. (1990). Non-Acoustic Communication in Small Cetaceans: Glance, Touch, Position, Gesture, and Bubbles.In *Sensory Abilities of Cetaceans* (pp. 537-544). New

York, NY: Springer.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences*, *98*(10), 5937–5942. https://doi.org/10.1073/pnas.101086398

Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, *22*(4), 966–978. https://doi.org/10.1111/j.1748-7692.2006.00082.x

Sharpe, F. A., & Dill, L. M. (1997). The behavior of Pacific herring schools in response to artificial humpback whale bubbles. *Canadian Journal of Zoology*, *75*(1982), 725–730. https://doi.org/10.1139/z97-093

Stankowich, T., & Coss, R. G. (2007). The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. P*roceedings of the Royal Society of London B: Biological Sciences*, *274*(1607), 175–182. https://doi.org/10.1098/rspb.2006.3716

Tamaki, N., Morisaka, T., & Taki, M. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioural Processes*, *73*(2), 209–15. https://doi.org/10.1016/j.beproc.2006.05.010

Thewissen, J. G. M. (1994). Phylogenetic aspects of Cetacean origins: A morphological perspective. *Journal of Mammalian Evolution*, *2*(3), 157–184. https://doi.org/10.1007/BF01473527

Thewissen, J. G. M., Cooper, L. N., Clementz, M. T., Bajpai, S., & Tiwari, B. N. (2007).

Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature*, *450*(7173), 1190–1194. https://doi.org/10.1038/nature06343

van der Woude, S. E. (2009). Bottlenose dolphins (*Tursiops truncatus*) moan as low in frequency as baleen whales. *The Journal of the Acoustical Society of America*, *126*(3), 1552. https://doi.org/10.1121/1.3177272

Visser, I. N., Smith, T. G., Bullock, I. D., Green, G. D., Carlsson, O. G. L., & Imberti, S. (2008). Antarctic peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science*, *24*(1), 225–234. https://doi.org/10.1111/j.1748-7692.2007.00163.x

Wiley, D., Ware, C., Bocconcelli, A., Cholewaik, D., Friedlaender, A., Thompson, M., & Weinrich, M. (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, *148*(5), 575–602. https://doi.org/10.1163/000579511X570893

Wood, F. G. (1953). Underwater Sound Productin and Concurrent Behavior of Captive Porpoises, *Tursiops truncatus* and *Stenella plagiodon*. *Bulletin of Marine Science of the Gulf and Caribbean*, *3*(2), 120–133.

Zaeschmar, J. R., Dwyer, S. L., & Stockin, K. A. (2013). Rare observations of false killer whales (Pseudorca crassidens) cooperatively feeding with common bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf, New Zealand. *Marine Mammal Science*, *29*(3), 555–562. https://doi.org/10.1111/j.1748-7692.2012.00582.x

Zahavi, A. (1975). Mate selection-A selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214. https://doi.org/10.1016/0022-5193(75)90111-3