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Analysis of a Rough-Toothed Dolphin (Steno bredanensis) Introduction in a Human Care Setting

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ANALYSIS OF A ROUGH-TOOTHED DOLPHIN *(STENO BREDANENSIS)*

INTRODUCTION IN A HUMAN CARE SETTING

by

Lindsey E. Johnson

A Dissertation
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Approved by:

Dr. Lucas Keefer, Committee Chair
Dr. Heidi Lyn
Dr. Richard Mohn
Dr. Elena Stepanova

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ABSTRACT

Rough-toothed dolphins are a rarely studied species of cetaceans found in temperate and tropical waters throughout the world. These dolphins live in fission-fusion societies and are highly social, swimming in tightly-packed and highly synchronized subgroups consisting of 2–10 individuals. The current study documents the introduction of a stranded calf into an existing population of six rough-toothed dolphins living in a human care setting. Specifically, recordings of vocal and non-vocal behaviors were analyzed across the four phases of the study: baseline, day of introduction, post-introduction, and follow-up. Whistles, a vocal signal associated with social contexts, increased from baseline to post-introduction phases (after an initial drop on the day of introduction) for both the new dolphin and the resident group. Non-vocal social behaviors showed the same pattern. Finally, whistle production was associated with social behaviors when considering all of the phases, but the association only held for the baseline condition when the relationship was assessed within each phase. This research helps to build knowledge about how this little-known species navigates the formation of new relationships and may inform procedures for future dolphin introductions.

ACKNOWLEDGMENTS

DEDICATION

I would like to dedicate this project to my late father, Carl Johnson, and brother, Darr Johnson, who both inspired me to be the person I am today. I am forever grateful for their undying love and guidance throughout my life.

I would also like to thank my brother, Dr. Thor Johnson, for believing in me and supporting me throughout my life, especially during my graduate school career. My mother, Beverly Johnson, also deserves a very special thank you as she has been there with grace, love, and kindness through every moment of joy, stress, and pain. My appreciation for all of my incredible family members is impossible to capture with words.

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CHAPTER I - INTRODUCTION

Complex societies, such as fission-fusion societies, are rare in nature. Fission-fusion societies are characterized by fluid relationships where individuals spend time in various subgroups throughout the day and may spend long periods apart from individuals with whom they have close bonds (Ramos-Fernández, 2005). Apart from humans, a relatively small number of species navigate these dynamic social relationships in order to survive and reproduce, a few of which are spider monkeys (*Ateles geoffroyi*), African elephants (*Loxodonta africana*), chimpanzees (*Pan troglodytes*), spotted hyenas (*Crocuta crocuta*), and several species of cetaceans (ex., *Tursiops truncatus, Sousa chinensis,*) (Ramos-Fernández, 2005; Poole, Tyack, Stoeger-Horwath, & Watwood, 2005; Goodall, 1986; Smith, Memenis, & Holekamp, 2007; Connor et al., 2000; Parra, Corkeron, & Arnold, 2011).

Vocal and non-vocal behaviors facilitate communication between individuals, enabling them to negotiate the fluid relationships found in fission-fusion societies. These relationships between various dyads tend to differ in quality. Some pairs may have an affiliative relationship where comforting tactile behaviors are frequent, while other dyads may have a more contentious relationship, characterized by aggressive behaviors. These existing relationships can sometimes influence interactions with other subgroups, e.g., Ramos-Fernandez (2005). Ramos-Fernandez (2005) hypothesized that spider monkeys use vocalizations to broadcast their identity to other subgroups out of visual range. He conducted a playback experiment which broadcast known individuals' calls in the wild and found that only subgroups consisting of close associates to the recorded vocalizer approached the speaker. Approaches to the vocalizer appeared to be impacted by existing

bonds. Bottlenose dolphins are also known to produce vocalizations that contain identity information, signature whistles. Subgroups that are out of visual range exchange signature whistles before they converge into one larger group (Quick & Janik, 2012). These vocal exchanges may serve a similar function in dolphins as they do in spider monkeys.

Both non-vocal and vocal behaviors facilitate the formation and dissolution of relationships, but the ways in which these behaviors are used to navigate these complex relationships remains understudied in cetaceans, particularly in one species known as the rough-toothed dolphin (*Steno bredanensis*). The purpose of the current study is to examine how a group of rough-toothed dolphins use vocalizations and social behaviors throughout a dynamic social situation: an unfamiliar conspecific being introduced to an established group of resident dolphins living in a human care setting (i.e., a zoological facility). The results of this study will help elucidate the manner in which rough-toothed dolphins form new relationships which, in turn, may inform husbandry policy on future animal introductions as well as having the potential to inform conservation efforts in the wild.

Bottlenose Dolphin Introductions in Human Care Settings

Many types of cetaceans are known to live in fission-fusion societies, but the ways in which bottlenose dolphins (*Tursiops truncatus)* negotiate relationships in fluid societies have received the majority of attention. One reason for this bias is the ease with which they live and reproduce in human care settings (Leatherwood & Reeves, 2012). This adaptability on the part of bottlenose dolphins has allowed zoological facilities world-wide to house populations of these animals. While populations of other species of

cetaceans are maintained in human care, bottlenose dolphins are by far the most common (Ceta Base, 2019). This ease of access allows researchers permanent, long-term access to known individuals and the opportunity to obtain accurate measures of vocal and non-vocal behavioral patterns that may accompany relationship formation and maintenance. One especially relevant context relating to the formation of new relationships in fission-fusion societies is when unfamiliar conspecifics merge into resident populations in a human care setting.

Because dolphins have lived in human care settings for nearly a century, there have been many instances of animals introduced into established populations. Unfortunately, formal reports of the process are rare, even with this well-studied species. The existing literature contains predominately early descriptive accounts of newly captured individuals being introduced to already domesticated animals. Vocalizations are largely ignored as the focus was on describing non-vocal behavioral exchanges. Aggression and agonistic reactions were frequently reported, including incidents where residents hurt and even killed the new animal (Caldwell & Caldwell, 1977; McBride, 1940; McBride & Hebb 1948). Sexual interest has been another response to the integration of new conspecifics with males trying to engage with unfamiliar females introduced into their habitat. One report described the dominant males displaying erections and remaining close to an iron gate separating an unfamiliar female even before even visual contact was possible (McBride & Hebb 1948). While these reports provide anecdotal descriptions of introduction events, quantitative studies are rare.

A recent study of a stranded bottlenose dolphin (a young male around 6 years old) being introduced to a resident pod (one female and one male, both over 30 years old) was

the first introduction study to incorporate acoustic analyses along with a systematic examination of changes in non-vocal behavior (Broadway, 2017). Bottlenose dolphins are known to produce learned vocal signals called signature whistles which broadcast the identity of the whistle producer. The patterns of signature whistle production and co-occurring behaviors throughout the introduction were the focus of her study. The research design pioneered by Broadway (2017) provides a quantitative method for analyzing both vocal and non-vocal behavior throughout the introduction process. As such, the current project follows her methodology as closely as possible. Consistency across studies will also allow for between-species comparisons.

The Broadway (2017) report of a bottlenose dolphin introduction in human care yielded some unexpected results. As whistles are a communicative signal, they were predicted to increase after the new individual was introduced to the 2 residents. While overall whistle production was greater than 200 whistles per hour during the baseline phase (primarily as a result of new dolphin, Chance), this rate dropped significantly on the day of introduction. This surprising result may be attributed to Chance's individual response to stress, or the age of the individuals he was being introduced to. Whistle rates eventually returned to baseline during the post-introduction and follow-up phases, suggesting that the situation was no longer perceived as stressful to the new individual.

In terms of signature whistles in particular, the new dolphin's signature whistle was the whistle most frequently produced throughout all phases except the day of the introduction, when it was the whistle least frequently produced. This pattern did not support the author's hypothesis that signature whistle rates would increase on the day of introduction, which is typically observed when groups of dolphins meet in the wild

(Quick & Janik, 2012). Again, this was interpreted as the new dolphin's individual reaction to the stress of the introduction. Throughout the majority of the study, the resident dolphins were physically separated from the new dolphin by a gate, though visual and acoustic contact was still possible. During the few occasions where the resident dolphins had the opportunity to physically interact with the new dolphin, no change in signature whistle rate was observed.

The two resident dolphins in the Broadway (2017) study showed different behavioral reactions than the new individual. The adult female showed interest in Chance, engaging in extended periods of spy-hopping on the day of the introduction. Her signature whistle rate was the only one to increase after the introduction, providing partial support for the author's original hypothesis. The adult male largely ignored the new individual, with his signature whistle rate increasing only slightly post-introduction. Neither of the resident dolphins showed any drastic behavioral changes throughout the post-introduction phases, while the new dolphin did show an increase in circle swimming, a stereotypical behavior sometimes associated with stress, and a decrease in object play.

Counter to Broadway's (2017) prediction that social behaviors would increase after the introduction, no changes in social behaviors occurred throughout the phases of the study and no agonistic behaviors were observed, results which do not mirror previous reports of introductions in human care. These discrepancies with previous accounts could possibly be attributed to the low number of resident dolphins, individual differences in personality, differences in age between the two adult residents and the new juvenile, and/or the presence of a gate which limited physical contact between the residents and the

new dolphin. As the author's analysis was largely exploratory in nature, more research is needed to determine if her results exemplify a typical cetacean introduction.

Rough-Toothed Dolphin Behavior

While rough-toothed dolphins live in fission-fusion societies, like other delphinids, these cetaceans have received less notice simply because there are far fewer populations in human care settings. Deep-water species such as the rough-toothed dolphins, are less accessible than shallow-water species in the wild and do not tend to reproduce as easily in human care as the bottlenose dolphins (Jefferson, 2018). As a result, the vast majority of what we know about this species has been garnered from in situ research that carries many limitations including sporadic access to the study population, limited visibility to behaviors that occur beneath the water's surface, and a lack of control over myriad variables. Regardless of these limitations, researchers have been able to outline some general characteristics of this species.

Rough-toothed dolphins are a pelagic species found in warm and temperate waters around the world. While this species is commonly reported to inhabit deep waters, preferring waters that are >1500 m in depth, some researchers have noted that their range can extend to shallow coastal waters as well (Baird, Webster, Mahaffy, McSweeney, Schorr, & Ligon, 2008; Kuczaj &Yeater, 2007; Ritter 2002). While they often inhabit waters of great depth and engage in deep dives, rough-toothed dolphins spend much of their time foraging near the surface (Baird et al., 2008). Multiple studies have found that rough-toothed dolphins feed primarily on fish living near the surface and surface-active behaviors such as leaping and tail slapping are common with feeding (Ritter, 2002).

Many researchers have noted the highly social nature of rough-toothed dolphins (Kuczaj & Yeater, 2007; Ritter, 2002). One reason for this characterization results from their social organization. This species of dolphin frequently swim together in tightly spaced subgroups, ranging from 2-10 individuals, who are highly synchronized in their movements (Baird et al., 2008; de Boer, 2010; Jefferson, 2018). This synchronization is thought to not only strengthen social bonds by affording opportunities for tactile contact, it may also reduce an individual's energy expenditure by reducing hydrodynamic drag (Kuczaj & Yeater, 2007; Götz et al., 2006). Energy may also be saved while swimming in tight subgroups by eliminating the need for each individual to echolocate. Götz, Verfuß, and Schnitzler (2005) suggest that these characteristic groupings may allow most individuals in the group to rely on the echolocation of one individual: When the dolphins swam in synchronized subgroups, one dolphin echolocated 80% of the time. In contrast, when swimming asynchronously (in a more dispersed and random pattern) there was always more than one dolphin producing clicks used in echolocation. The dolphins' limited their own click production when it was possible to gain information about the environment by "eavesdropping" on the echoes of clicks produced by a single individual in the group. While the dolphins may use this technique to save energy, this scenario also provides evidence that dolphins are capable of engaging in a key aspect of social communication, joint attention (Janik, 2013).

Rough-toothed dolphins frequently utilize social contact, or tactile behavior, as one way to navigate the complex relationships in their fission-fusion society. Kuczaj and Yeater (2007) highlight this fact, detailing the frequent occurrence of a specific tactile behavior: pectoral fin contact (i.e., one dolphin touches another dolphin with their

pectoral fin). De Boer (2010) also reported frequent use of pectoral fin rubbing during social interactions between rough-toothed dolphins. Kuczaj & Yeater (2007) emphasized the importance of physical contact within this species as this type of contact often accompanies the tightly spaced, synchronous swim pattern that is so frequently reported in the literature. This type of contact is currently understood as affiliative in this and other delphinid species, helping to affirm and strengthen social bonds that are essential for survival (Dudzinski & Ribic, 2017; Kuczaj & Yeater, 2007).

Play is often present in highly social species and is thought to function as a way of learning about social communication and developing bonds with various individuals (Kuczaj & Eskelinen, 2014). Rough-toothed dolphins are known to engage in object play, picking up pieces of plastic or seaweed to carry or pass between one other (De Boer, 2010; Kuczaj & Highfill, 2005; Kuczaj and Yeater, 2007). Rough-toothed dolphins' playfulness is also evident when considering the frequent reports of approaching the research vessels and even bow- or wake-riding (Jefferson, 2018; Kuczaj & Yeater, 2007). Kuczaj and Yeater (2007) describe these dolphins inspecting the propeller of the research vessel as well as the hydrophones that were collecting acoustic data.

Rough-toothed dolphins negotiate social relationships not only within their own species, but with other species as well. There are numerous reports of this species interacting with other cetacean and non-cetacean species including many different varieties of cetaceans, birds, and fish. Many authors have noted that rough-toothed dolphins swim in intermingled groups with species such as melon-headed whales and false killer whales (Baird et al., 2008). Interactions with seabirds and fish are common and often include surface feeding scenarios where multiple species are converging to

consume a bait ball composed of thousands of prey fish (Baird et al., 2008). Rough-toothed dolphins have also been reported to use other species as play objects; in one incident, several individuals pushed a turtle around repeatedly at the surface of the water (Ritter, 2002). Swimming in close proximity to, feeding with, and playing with animals of various species suggests rough-toothed dolphins' social behaviors are characteristic of both within and between species interactions.

Vocal Behavior of Rough-Toothed Dolphins

Rough-toothed dolphins produce three categories of vocalizations common to many delphinid species (whistles, burst pulses, and echolocation clicks), but the majority of past research has been concentrated on whistles (Herzing, 1996; Oswald, Rankin & Barlow, 2008). Researchers have determined the characteristic parameters of rough-toothed dolphins' whistles via studies with wild populations. It is worth noting that past research has largely focused on the species-specific parameters of whistles as opposed to an emphasis on the behavioral contexts that co-occur with that vocalization.

Whistles are continuous, narrow-band, frequency modulated signals used primarily in social communication in many species of cetaceans (e.g., Dudzinski, 1996). Whistles vary across species and research has demonstrated general trends in rough-toothed dolphin whistles, while acknowledging some within species variation (Oswald et al., 2008; de Lima, de Andrade, Ramos de Carvalho, Lailson-Brito, & de Freitas Azevedo, 2012). Rough-toothed dolphin whistles are generally low in acoustic frequency and short in duration. See Figure 1 for an example of a spectrogram displaying a rough-toothed dolphin whistle. Evans (1967) recorded whistles ranging from 3–10 kHz, while de Lima et al. (2012) reported rough-toothed dolphin whistles tend to be below 14 kHz,

with 78.8% of whistles having a frequency range between .23–2.98 kHz. In contrast, the average frequency range for delphinid species in general is 2–20 kHz, with some species emitting fundamental frequencies close to 35 kHz (Lammers, Au, & Herzing, 2003; Oswald et al., 2008). Rankin et al. (2015) noted that rough-toothed dolphin whistles have an average duration of 0.7 s. Other estimates fit this pattern: Evans (1967) recorded whistles lasting from 0.1–0.9 sec, Busnel and Dziedzic (1966) reported durations from 0.38–0.61s, and de Lima et al. (2012) noted that 89.7% of rough-toothed dolphin whistles were shorter that 600 ms. This duration is on the very low end of whistle durations in all delphinid species, with typical ranges between several tenths of a second to several seconds (Tyack & Clark, 2000).

Figure 1

Spectrogram of a Rough-Toothed Dolphin Whistle
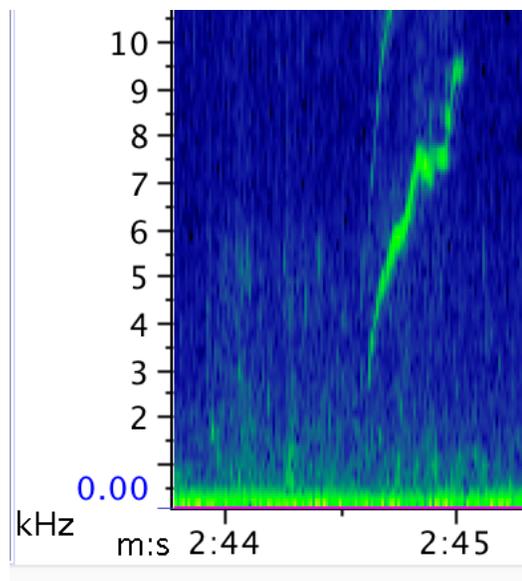
Note. Frequency is displayed on the y-axis and time on the x-axis.

Rough-toothed dolphin whistles are also characterized by their frequent stepped or segmented nature. Many stepped whistles consist of an overall ascending pattern with

ending frequencies being greater than beginning frequencies, but within each step, the frequency decreases. This pattern is common in whistles from rough-toothed dolphins, but is rarely seen in other species (Rankin, Oswald, Simonis, & Barlow, 2015). Rankin et al., (2015) reported most whistles contain at least one step, with the average being 1.5 steps per whistle (Rankin et al., 2015), while de Lima et al., (2012) note that the most common whistle type is of a constant frequency, lacking any segments (33.8% of all whistles), but segmented whistles were emitted at nearly the same rate (28.5%). Belikov and Bel'Kovich (2007) noted an association between segmented beluga calls and long-range communication, and de Lima et al. (2012) theorized that these types of calls may serve the same function in rough-toothed dolphins based on their typical pattern of swimming involving multiple subgroups separated by large distances.

While research with wild populations has informed our knowledge of the average parameters of these communicative signals, these studies are not able to incorporate long-term observations of known individuals in multiple behavioral contexts. These types of studies are nearly impossible to conduct in the wild, due to the dolphins' habitat, but are possible when scientists have access to populations in a human care setting.

Research in Human Care Settings

While much has been gained from research with wild rough-toothed dolphin populations, research conducted in a human care setting offers advantages that can help to fill in the large gaps of knowledge that persist regarding this species. Research with human care populations complements studies in the wild and helps to build a more complete understanding. For example, Xitco and Roitblat (1996) conducted an experiment with captive bottlenose dolphins which determined that species could

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recognize objects by eavesdropping on a conspecifics' echolocation. This finding prompted Götz, Verfuß, and Schnitzler (2005) to theorize that rough-toothed dolphins use the same technique when swimming in their characteristically tight, highly synchronized, subgroups.

Research in a human care setting offers other important advantages including the possibility for longitudinal observations with known individuals, predictable access to the research population, controlled settings that provide the opportunity to assess higher-level cognitive functioning, the ability to implement experimental paradigms, and methodology that combines visual data (on individual or group behavior) with acoustic recordings. These advantages have allowed systematic research designs that have illuminated various aspects of rough-toothed dolphin's social behavior.

The limited number of studies conducted with rough-toothed dolphins in human care may be due to extremely small number of animals residing in that setting; there are currently two facilities in North America housing rough-toothed dolphins. Interestingly, much of the recent work with captive animals of this species has involved many of the animals in the current project. One of those studies involved an analysis of the social interactions of the rough-toothed dolphins that were housed at Gulf World Marine Park, specifically focusing on the only two juvenile male dolphins in the population at the time, Ivan and Astro (Hanna, 2016). Ivan was the more dominant of the two dolphins, consequently he determined how much time the two spent together by initiating and ending their social interactions. Ivan and Astro had the most affiliative social interactions (social touch and social swims) out of every pair, but also had a high number of sexual and aggressive interactions between them. When aggressive behavior occurred in the

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habitat, Ivan and Astro most often responded with affiliative behaviors with each other, while all other dolphins tended to respond with more aggression.

Another study conducted with the population of rough-toothed dolphins housed at Gulf World examined the effects of environmental enrichment objects (e.g., toys such as balls or rubber hoses) on various types of social behavior including tactile and non-tactile behavior classified as either affiliative or aggressive in nature (Caffrey, 2013). When the dolphins had access to enrichment objects, the total number of both aggressive and non-aggressive social behaviors was reduced. Aggressive social behaviors were defined as hits and rakes/bites (tactile) plus the chase behavior (non-tactile). While chasing has been observed in both play and aggressive contexts (Dudzinski, 2010), Caffrey justified her classification of chasing as aggressive by reporting that most tactile aggressive behaviors observed were preceded by a chase. All aggressive behaviors were initiated by one of the four juveniles (Astro, Ivan, Largo, and Dancer) potentially as a way to establish their place in the dominance hierarchy. Non-tactile social behavior (e.g., pair swim, group swim, follow, pair/group rest, chase) was also greater in the non-enrichment condition, likely due to the opportunity for different types of social interaction (e.g., mutual object play) during the enrichment condition. Affiliative tactile behavior (touch, rub, contact swim, sexual contact) remained unchanged when enrichment was present. No sex differences were observed in this study, though significant individual differences were present in most of the analyses. Interestingly the only sexual behaviors noted throughout the study involved Astro and Ivan, the two dolphins with the highest rates of association out of all other dyads in the population (Hanna, 2016). The authors concluded that

interacting with enrichment objects may not be a suitable replacement for dolphin-to-dolphin social affiliative behaviors, but may reduce aggressive interactions.

Research with human care populations has also helped elucidate some differences between rough-toothed and bottlenose dolphins. The population at Gulf World was the subject of an experimental investigation of dolphins' reactions to surprising and expectation-violating situations (Lilley, de Vere, Yeater, & Kuczaj, 2018). Both rough-toothed and bottlenose dolphins spent more time looking at a moving and variable stimulus (a jack-in-the-box) than a control condition (a static cylinder). While individual differences were prevalent within each species, the authors reported several species-level differences. The rough-toothed dolphins looked at all of the stimuli twice as long as the bottlenose dolphins, suggesting possible differences in curiosity between species. Also, the rough-toothed dolphins displayed less open mouth behaviors than the bottlenose dolphins. In past studies, open mouth behaviors have been correlated with other aggressive behaviors such as jaw claps, head-to-head interactions, and chasing (Overstrom, 1983), but these other aggressive behaviors were absent in Lilley et al. (2018). This result parallels some authors' suggestions that an open mouth may be used in excitement or play contexts and not solely during aggression (Dudzinski, 1998; Marten & Psarkos, 1995). Additionally, the rough-toothed dolphins produced more bubble trails than their bottlenose counterparts. Bubble trails often accompany dolphin vocalizations, particularly whistles (McBride & Hebb, 1948), but vocals can also be produced by dolphins without an accompanying bubble trail (Fripp, 2005). Lilley et al. (2018) did not include any acoustic recordings in their analyses so it could not be determined if the

greater number of bubble trails observed with the rough-toothed dolphins indicated that species was producing more vocalizations than the bottlenose dolphins.

An additional cross-species comparison was conducted with the Gulf World population examining factors that relate to interest in a video (Winship, 2016). Paralleling the results of Lilley et al. (2018), the author reported several species-level differences. Rough-toothed dolphins engaged in more bubble and interest behaviors, while the bottlenose dolphins displayed more aggressive behaviors. In terms of gender differences, bottlenose dolphin males were more likely to show interest in the video than the females, but rough-toothed dolphin females showed more interest than the males. A final species-level difference was that rough-toothed dolphins would interact with the video independently, but bottlenose dolphins tended to interact with the video with one or more conspecifics. While individual differences within each species were prevalent in the study, as with Lilley et al. (2018) and Caffrey (2013), the presence of species-level differences highlights the need for continued research with rough-toothed dolphins.

Rough-Toothed Dolphin Introductions in Human Care Settings

Regarding the specific social context of forming relationships with unknown conspecifics, Yeater, Miller, Caffery, and Kuczaj (2013) provide one of the only quantitative reports documenting introductions in rough-toothed dolphins. Two groups residing at Gulf World Marine Park were unfamiliar with each other with the exception of Doris (adult female) and Ivan (juvenile male) who stranded together. In 2006, the two subgroups of 3 individuals each were combined to create one population of 6 animals. Social behaviors included symmetrical social behaviors (i.e., no clear initiator/receiver) of pair swim, social play, and group social ball (i.e., two or more dolphins engaging in

fast, non-directional swimming and "appear to be wrestling") and asymmetrical social behaviors of nonsexual contact behavior, sexual contact behavior, chase behavior, and aggressive behaviors (e.g., hit, mouth/bite, and threat—touching lateral side to another dolphin's lateral side). Interaction rates were determined for the time periods before and after the move and indicated social relationships that were present before the integration persisted into the new social landscape, but new relationships were also formed.

The results of this study noted several important patterns. Ivan and Largo (juvenile female) engaged in the most symmetrical social behavior both pre and post move. Pre-move, the most nonsexual social behaviors and chases were initiated by Ivan towards Largo, but post-move Ivan initiated the most nonsexual social behaviors and chases towards Astro (juvenile male), a social partner that was not available pre-move. Due to the lack of aggressive behaviors in the pre-move phase, only post-move aggression was analyzed. It was found that Doris and Ivan were the most dominant individuals in terms of aggression, both frequently initiating toward Astro, and Doris initiating toward Vixen (juvenile female). While the emphasis on changes in interaction rates provides key insights into rough-toothed behavior during this uncommon social situation, Yeater et al. (2013) did not collect any acoustic recordings. Therefore, it remains unknown how whistle production may be altered as a result of an increase in group size of a human care population of rough-toothed dolphins.

Purpose of Study

The goal of the current study is to enhance our understanding of how rough-toothed dolphins' vocal and non-vocal behavior change when an unknown conspecific is introduced to a group of established individuals. Archival data was used to analyze how

vocalizations are used in this extra-ordinary context, a question which has been only recently been studied in bottlenose dolphins (Broadway, 2017) and never with rough-toothed dolphins.

This project replicates the methodology used by Broadway (2017) as closely as possible to maximize the ability to compare results and examine where similarities and differences may exist between species. Specifically, Broadway (2017) divided the introduction process into several phases for the purposes of data analysis. The baseline phase consisted of 10 days of two 15-min observations of the two resident dolphins and the one new dolphin. The day of introduction was included as a separate category for analysis. The following phase included 10 days directly following the day of the introduction, known as the post-introduction phase. Finally, five additional days of follow-up data were collected over the three months following the introduction. Following this framework for data collection and analysis, the current project aimed to address several research questions:

Question 1: How does the behavioral budget change for the resident dolphins from baseline to post-introduction phases?

Due to the curious and social nature of the species, the introduction of a new conspecific would likely increase social behaviors (including social swims, social touch, and aggression) in the group as they become familiar with the new individual. As the number of individuals in a population increases, the number of opportunities for social interactions also increases.

H1: The behavioral budget of the resident dolphins was predicted to include more social behaviors during the post-introduction phases compared to the baseline phase.

Question 2: How does the resident dolphins' average whistle rate change from baseline to post-introduction phases?

An increase in whistle production has been associated with social contexts such as non-directional swimming (variable swim patterns within the pod, as opposed to the whole pod traveling in one direction for an extended time) (Quick & Janik, 2008), converging with other groups in the wild (Quick & Janik, 2012), and maintaining contact within mixed species groups (Oswald et al., 2008), therefore the social context of being introduced to unknown conspecifics would likely elicit increased rates of whistle production from both the resident dolphins and the new individual.

H2: The resident dolphins' average whistle rate was predicted to be greater during the post-introduction phases compared to the baseline phase.

Question 3: How does the new individual's whistle rate change from baseline to post-introduction phases?

Due to the new individual being housed in isolation from the time of her rescue to the time of her introduction to the resident pod, the opportunity for her to successfully communicate with conspecifics using whistles was not available to her during the baseline phase. Additionally methodological constraints dictate that whistles could only be localized to the new individual when she was physically isolated from the rest of the group. During the later phases, the new individual had

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already spent a substantial amount of time with the resident group and was in the process of forming and solidifying relationships with various individuals. Therefore she likely experienced stress during these periods of physical isolation. Whistle rates are known to increase when dolphins are separated from their pod (Esch, Sayigh, Blum, & Wells, 2009). Thus the new individual would likely produce whistles when she was physically isolated from the resident dolphins during post-introduction phases.

H3: The new individual's whistle rate was predicted to be greater during the post-introduction phases compared to the baseline phase.

Question 4: Does the relationship between whistle rate and non-vocal behavior change for the resident dolphins from baseline to post-introduction phases?

Whistles are primarily communicative signals that often are associated with social behavior (Cook et al., 2004). Therefore, whistles were likely used during the social behavioral contexts regardless of the number of individuals present.

H4: Whistle rates were predicted to positively correlate with the social behaviors of the resident dolphins during both the baseline and post-introduction phases.

Question 5: Does the relationship between whistle rate and non-vocal behavior change for the new individual from baseline to post-introduction phases?

Due to the new individual's isolation throughout the baseline phase, she did not have an opportunity to engage in any social behaviors. Additionally, methodological constraints dictated that whistles could only be localized to the new individual when she was physically isolated from the rest of the group. This physical separation limited her opportunities for social behavior (though some

social behaviors were possible through the gate), and increased the likelihood she whistled as a result of the stress of being isolated. When the new individual was in physical contact with the resident group (providing the most opportunity for social behaviors) any whistles she produced could not be differentiated from the group. These limitations would likely make this hypothesis nearly untestable.

H5: Whistle rates were not predicted to correlate with the social behavior of the new individual during any of the phases of the study

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CHAPTER II - METHOD

Subjects

The subjects in this study included 6 rough-toothed dolphins (3 males, 3 females) in the resident population at a marine mammal facility in Florida, as well as the new young female rough-toothed dolphin that stranded on the Mississippi coast shortly after Hurricane Michael in October 2018. See Table 1 for a list of subjects' sex and age class (approximate ages were used due to all of the animals being rescued from stranding events). Per Eskelinen et al. (2015), age classes are defined as: calf (0–2 years), juvenile (3–10 years), and adult (11+ years). Immediately after rescue, the new individual was housed at a marine mammal facility in Gulfport, MS for rehabilitation. The new dolphin spent approximately three months isolated in a medical pool at that facility before she was transferred to a medical pool at the facility in Florida in January of 2019. A hearing test was conducted and determined that the new individual had very limited hearing, mostly isolated to low frequencies. Three of the six resident rough-toothed dolphins also experienced similar (or more severe) hearing loss. As a result, the vocal behaviors of all individuals may be modified and/or limited. The new dolphin's integration into the resident population at the facility in Florida was the focus of the current study.

Table 1

Sex and Age Class of Each Subject

Dolphin	Sex	Age Class
Astro	M	Adult
Dagney*	F	Calf
Doris	F	Adult
Ivan	M	Adult
Kitana	F	Adult
Largo	F	Adult
Stan	M	Juvenile

Note. The new individual is indicated with the asterix.

Procedure

The research team collected data for a total of 25 days, over the course of four months, to compile a sufficient amount of data for the current study. To collect acoustic recordings, researchers placed a 4-channel hydrophone array in the rough-toothed dolphins' habitat for as long as possible each day of data collection (hydrophones had to be removed for public shows/interactive programs, sea lion training, and cleaning of the habitat). The array of hydrophones allows for each vocalization to be localized to a particular region of the habitat by determining which hydrophone the signal reached first. Researchers and staff coordinated the placement of the hydrophones to ensure the safety of the animals. The configuration is depicted in Figure 2. All hydrophones connected to a multi-channel digital recorder that transformed the audio into .wav files for analysis.

Figure 2

Rough-Toothed Dolphin Enclosure as Seen From Above
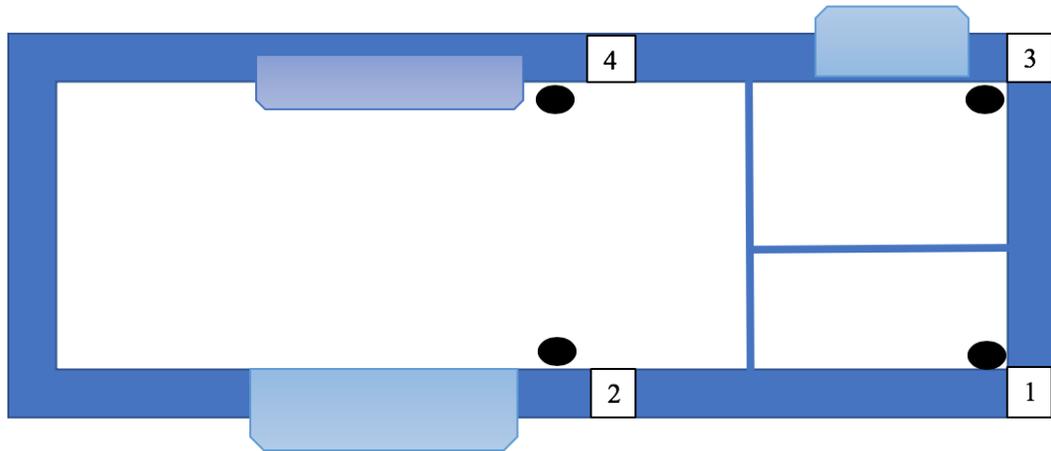
Note. The locations of the hydrophones are denoted with the black ovals, with numbers indicating the channel used for recording.

The research team collected behavioral data in accord with Broadway (2017), using paper ethograms and a stopwatch to record behavioral data from poolside. The behavioral observations were 15 minutes in duration and took place approximately twice daily for each dolphin (two dolphins were observed via focal follow during the same 15-minute observation session). The timing of these recordings was counterbalanced across time of day and included observations before the first feed of the day, after the last feed of the day, and in between training sessions (see Table 2 for an example schedule utilized by Broadway (2017)). Daily public programs, sea lion training, and habitat cleaning limited adherence to a pre-planned schedule, though counterbalancing across time of day was still achieved. Researchers did not conduct behavioral observations unless these conditions were met: all residents had physical access to each other, no focal dolphins

could be involved in a training session, and no cleaning equipment could be in use. They

noted if any trainer interactions occurred outside of formal training sessions.

Table 2

Example of Weekly Schedule

Day	7-9:00am	9-11:00am	11:30-1:30	1:30-3:30pm	3:30-5:30pm	5:30-7:30pm
Monday	X		X			
Tuesday				X		X
Wednesday		X			X	
Thursday			X			X
Friday	X	X				
Saturday				X		

The behaviors included in this study can be divided into two broad categories:

swim behaviors and secondary behaviors. Swim behaviors include habitat usage (i.e.,

where the dolphins are located), swim speed, swim pattern (e.g., circular or irregular

swim pattern), and social swim (swimming with one or more conspecifics). Secondary

behaviors included social interactions (e.g., touching, orienting, or responding to other

individuals), object play, and aggression. They noted if any unusual behaviors occurred

that did not fit in any of the defined categories. Swim behaviors were recorded every 60

seconds during focal follows using instantaneous sampling. Secondary behaviors (and

social swims) were recorded as present or absent during each 60 second interval throughout each focal follow. Definitions of swim and secondary behaviors are listed in Table 3.

Table 3

Definitions of Swim and Secondary Behaviors to be Recorded During Behavioral Observations

Swim Behaviors	Definition
Circle swim	A dolphin swimming in a repetitive pattern. This typically includes circling the perimeter of the enclosure, but could include any repetitive swim pattern.
Non-circle swim	A dolphin is swimming in irregular patterns around the pool
Social swim	Two or more dolphins swimming and surfacing in sync near one another
Stationary	Dolphin is non-mobile, resting in one position at or near the surface
Slow	Typical swim speed
Fast	Swimming faster than normal speed for more than 5 seconds

Secondary behaviors	Definition
Social Touch	One dolphin is in physical contact with the other with no evidence of aggression (no biting, raking or charging).
Object Play	A dolphin is in physical contact with an object for more than 1 second.
Aggression/ displacement	One dolphin bites, rakes, or charges another. One dolphin attempts to enter a pool area and is blocked by the other. This also includes instances of tail and chin slaps on the surface of the water as well as open mouth behaviors not directed at a trainer.

During the first 5 days of data collection, the resident group and the new individual were observed in their two separate enclosures. These observations served as a baseline for comparison. The second phase of observations began the day of the introduction. Acoustic recordings began approximately one hour before the introduction began, and continued for ~9 hours post-introduction. The remaining observation periods

25

proceeded with the schedule that was established during baseline. All observations were organized into 4 phases for analysis (see Table 4).

Table 4

Duration and Number of Observations in Each Phase of the Study

Phases of Study	Duration	Number of Observations (per dolphin in resident group)	Number of Observations (new individual)
Baseline	5 days (over 2 months)	4 or 5	4
Day of Introduction	1 day	1 or 2	2
Post-Introduction	10 days (over 1st month)	16–18	17
Follow up	8 days (over 2nd–4th month)	10 or 11	11

Statistical Analyses

Acoustic data was analyzed using Raven Pro version 1.5 Interactive Sound Analysis Software. EXCEL was used to code behavioral and acoustic data in preparation for analysis. Finally, IBM SPSS Statistics version 26 was used to conduct the statistical analyses once the data was coded.

Acoustic Analyses

To determine which dolphin was whistling (resident group vs. new individual), whistles were be localized by determining which of the hydrophones displayed the signal with the greatest amplitude (López-Rivas & Bazúa-Durán, 2010). As an example, in the early days of the introduction, the new dolphin was physically isolated (though visual and acoustic contact was possible) in the smallest of the three areas of the enclosure (next to Channel 1) while the other dolphins had access to the main area (closest to Channels 2 or 4). If a vocalization appeared loudest on Channel 1, it would have been produced by the

new dolphin, but if it appeared loudest on Channels 2, 3, or 4, the sound would have come from a member of the original group.

H1

A series of Pearson's chi-square tests were used to assess the prediction that the resident dolphins will display more social behaviors during the post introduction phases than the baseline phase. Specifically, the number of intervals where social behavior was present was calculated for each phase. The percentage of intervals where social behaviors were present in the resident dolphins was then compared across each phase (Baseline, Day of Introduction, Post Introduction, Follow Up).

H2

A chi-square test was performed to interpret differences in whistle production across phases of the study. Specifically, the chi-square test was used to analyze potential differences in the percentage of intervals containing whistles across the four phases. The resident dolphins' average whistle rate (number of whistles per minute per dolphin) was also calculated for each observation as another way to conceptualize the data. Whistle rate serves as a useful descriptive to understand how across whistle production changed across the various phases of the study.

H3

To assess if the new individual's whistle rate was greater during post-introduction phases than baseline, a chi-square test identified any potential differences in the percentage of intervals containing whistles across each phase. The new dolphin's whistle rate was also calculated for descriptive purposes.

H4

Whistle production for the resident dolphins was predicted to be positively related to social behaviors occurring in the group. To evaluate this prediction each interval a social behavior occurred was analyzed to identify if whistle production was present or absent. The number of intervals containing both a whistle and a social behavior was compared to the number of intervals containing a whistle without a social behavior for each phase of the study. These comparisons were analyzed within each phase using chi-square tests.

H5

The new dolphin's whistle production was not predicted to be associated with social behaviors during any of the phases. Intervals with whistles and social behaviors were compared to intervals with whistles no social behaviors within each phase using chi-square tests, when possible.

CHAPTER III - RESULTS

There were a total of 76 behavioral observations for the resident dolphins (1216 intervals) and 14 behavioral observations for the new dolphin (224 intervals) included in the statistical analyses (see Table 5). These observations were collected across 40

Table 5

Observation Sessions Included in Statistical Analyses

Phases of Study	Duration	Number of Sessions (residents)	Number of Sessions (new individual)
Baseline	4 days (over 2 months)	12	4
Day of Introduction	1 day	4	2
Post-Introduction	5 days (over 2 weeks)	12	4
Follow-Up	6 days (over 2nd– 4th month)	12	4
Total	16 days (over 5 months)	40	14

observation sessions (two resident dolphins were observed per session for the majority of sessions) over 16 data collection days, spanning 5 months. Twelve sessions from the post-introduction and follow-up phases were selected for the resident dolphins' analyses to match the number of sessions obtained in the baseline condition (4 sessions for the new dolphin). Observation sessions were eliminated if trainers were in the water and whistles could not be differentiated from the noise of their rubber shoes, if resident dolphins were separated from each other (excluding one session in the follow-up phase), or if there were technical issues with the hydrophones, camera, or clock synchronization. After unusable sessions were eliminated, the first twelve sessions were selected from each phase for analyses (4 in the case of the new individual).

Of the 1216 total intervals for resident dolphins, 91 were excluded (7.5%) from the behavioral observations due to the focal dolphin not being observed in the allotted timeframe, a mid-observation feeding session, or a mid-observation gating session resulting in resident dolphins being separated into different habitats. Those intervals were removed from further analyses involving social behaviors, leaving a total of $N = 1125$ valid intervals for the residents. Observations of the new dolphin totaled 224 intervals, of which 68 were excluded (30.4%) from the behavioral analyses, resulting in $N = 156$ valid intervals. The vast majority ($n = 64$) were removed due to prosocial behaviors being impossible during baseline when she was in isolation, and the remaining four intervals were removed due to an impromptu feeding session.

Fewer intervals were excluded from the acoustic analyses ($n = 38$, 3.1% of resident dolphins' 1216 intervals) as it was possible to note if a whistle was detected by a hydrophone during a specific interval without physically seeing the focal dolphin. This left a total of $N = 1178$ intervals available for the residents' acoustic analyses. The excluded intervals involved instances of impromptu feeding sessions and/or gating sessions where the resident dolphins were separated from each other as well as instances when the whistle producer could not be determined. For the new dolphin, 7 intervals were excluded from acoustic analyses due to a squeegee being used in the habitat (making whistle-like noises) and an impromptu feeding session, resulting in $N = 217$ valid intervals.

Throughout all phases, resident dolphins engaged in social behaviors during 176 intervals (14.5%). In 137 of those intervals (12.1%), the residents were engaging in prosocial behaviors (social swims and/or social touches) and in 52 intervals (4.6%) the

residents displayed aggressive behaviors. In terms of whistle production, 279 intervals

(23.6%) contained at least one whistle produced by at least one of the resident dolphins.

The new dolphin engaged in prosocial behaviors during 33 intervals (21.2%), all

of which occurred during the follow-up phase (in observations when the new individual

was free-swimming with the resident dolphins, $n = 3$ observations). As mentioned above,

these prosocial behaviors were impossible during the baseline condition due to her

isolation and nearly impossible during the observations when she was physically—

though not visually or acoustically—separated from the residents by a grated gate, $n = 11$

observations. Throughout all of the new dolphin's behavioral observations, aggression

was only observed during two instances (0.9%): once during the post-introduction phase

when she performed an open mouth behavior at the hydrophone, and once during the

follow-up phase when she was being chased (two additional chases involving the new

dolphin occurred during resident's behavioral observations). Regarding the new dolphin's

whistle production across all phases, she produced at least one whistle during 15

intervals (6.9%).

H1: Resident Dolphins' Social Behavior by Phase

The resident dolphins engaged in different proportions of social behaviors across

the phases of the introduction, χ^2 ($df = 3$, $N = 1125$) = 12.02, $p = .007$, supporting **H1.**

However, this shift was relatively small as indicated by Cramer's $V = .103$. As indicated

in Figure 3, the resident dolphins engaged in the lowest proportion of social behaviors

during the day of introduction (9.4%) and highest during the follow up phase (21%).

Figure 3

Percentage of Intervals Containing Social Behaviors as a Function of Phase
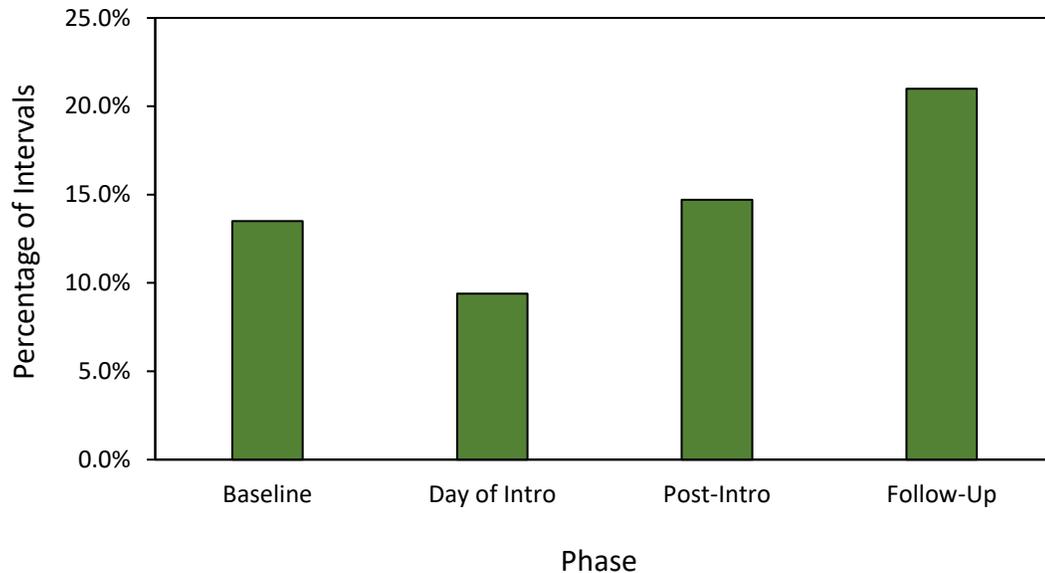
To further clarify the relationship between resident dolphins' social behaviors and phase of the study, prosocial behaviors and aggression were analyzed separately. The resident dolphins' prosocial behaviors were not related to phase, χ^2 ($df = 3$, $N = 1125$) = 5.06, $p = .17$, however their aggressive behaviors were related to phase, χ^2 ($df = 3$, $N = 1125$) = 16.73, $p = .001$, though the effect was small, Cramer's $V = .12$. The resident dolphins' proportion of prosocial behaviors ranged from a low of 7.7% ($n = 9$) on the day of introduction to a high of 14.9% ($n = 50$) during the follow-up phase, while their aggressive behaviors ranged from a low of 1.7% ($n = 2$) on the day of introduction to a high of 8.4% ($n = 28$) during the follow-up phase (see Figure 4).

Figure 4

Percentage of Intervals Containing Prosocial and Aggressive Behaviors as a Function of Phase
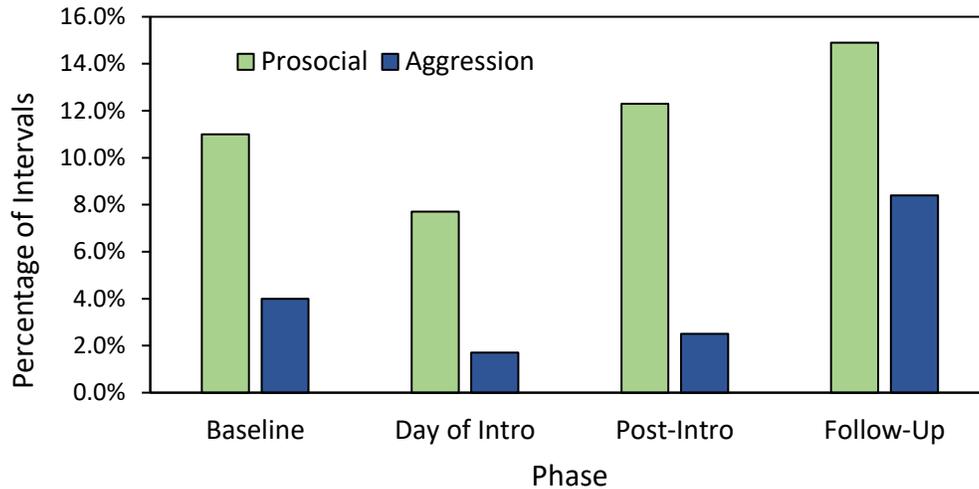
It is worth noting that of the 12 observation sessions included in the follow-up phase for resident dolphins, six occurred while the new individual was separated from the residents and the other six occurred while the new dolphin was free-swimming with the residents. During the sessions where the new individual was separate from the residents, the residents engaged in prosocial behaviors during 15 intervals (9.7%) and aggressive behaviors during 17 intervals (11%). This is in contrast to the percentages observed when the new dolphin was free-swimming with the group: 35 intervals (19.4%) included the residents engaging in prosocial behaviors and 11 intervals (6.1%) included aggressive behaviors.

H2: Whistle Production by Phase—Resident Dolphins

The resident dolphins' whistle production was significantly associated with the phase of the introduction, χ^2 ($df = 3$, $N = 1178$) = 21.57, $p < .001$, Cramer's $V = .14$,

providing support for **H2.** The residents' whistle production ranged from a low of 12%

on the day of introduction to a high of 29.7% during the follow up phase (see Figure 5).

Figure 5

Percentage of Intervals Containing a Whistle(s) Produced by a Resident Dolphin(s)

Across Phases
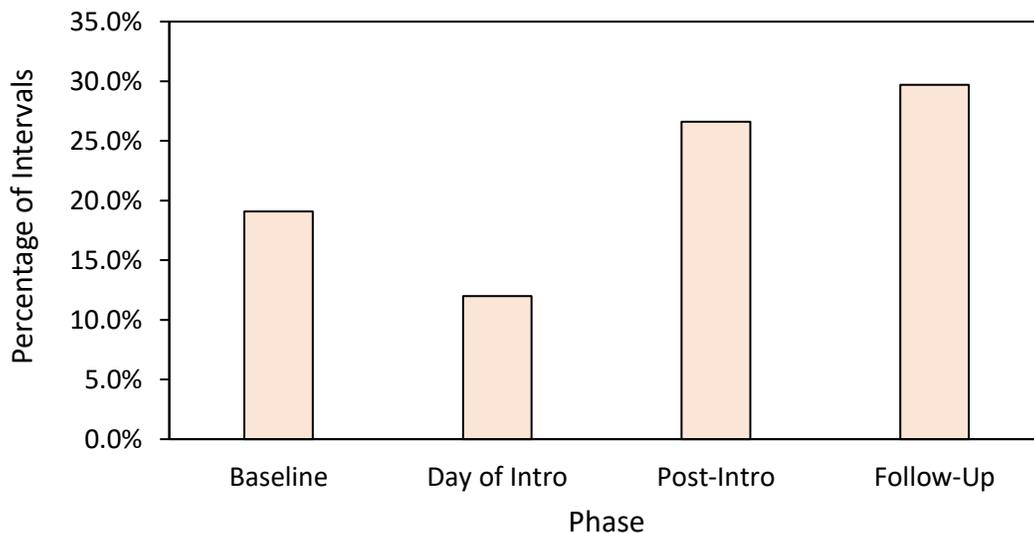
Whistle rates were also calculated for each observation session by first tallying

the number of whistles in that session. The total was divided by the number of minutes in

that session and then by the number of dolphins in the group. The resident dolphin's

mean whistle rate was the lowest during the day of intro ($M = 0.07$) and highest during

the follow-up phase ($M = 1.12$), as depicted in Figure 6.

A further breakdown of mean whistle rates by day of data collection reveals a low

of $M = 0.02$ on April 20th and a high of $M = .51$ on July 24th. The resident dolphins'

mean whistle rate for each day of data collection is displayed on Figure 7.

Figure 6

Resident Dolphins' Mean Whistle Rate by Phase
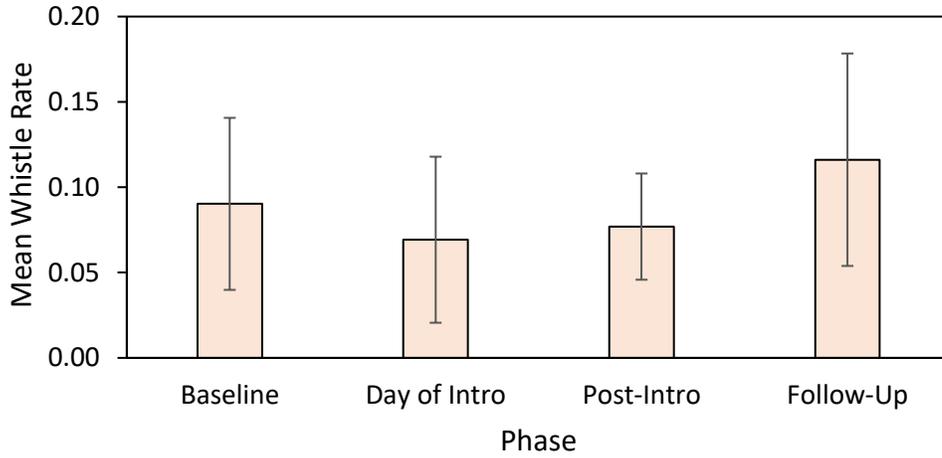
 Note. Error bars represent 95% confidence intervals.

Figure 7

Resident Dolphins' Mean Whistle Rate by Date of Data Collection.
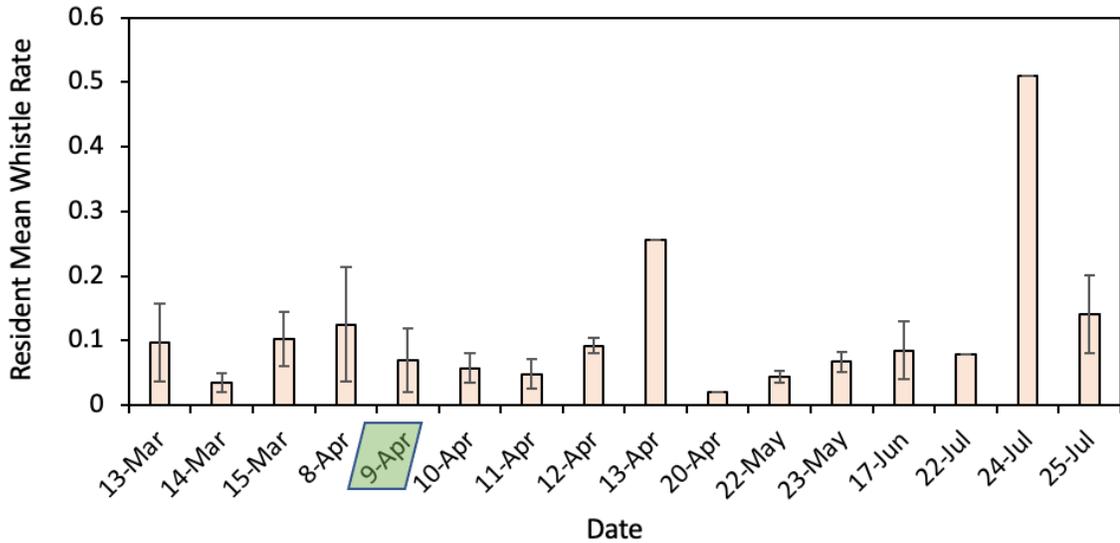
Note. The day of the introduction is highlighted in green. Error bars represent 95%

confidence intervals (bars without confidence intervals represent days with a single

observation session).

Within the follow-up phase, recall that half of the observation sessions occurred while the new dolphin was physically separated from the residents (as she was during day of intro and post-intro phases), but for the other half, she was free-swimming with the residents. Figure 8 displays the whistle rates for all of the follow-up sessions across both conditions. Descriptively, the mean whistle rate of the sessions when the new dolphin was interacting freely with the group was higher than when she was separate (new dolphin with group: $M = 0.19$, $SD = 0.18$; new dolphin separate: $M = 0.05$, $SD = 0.03$).

Figure 8

Resident Dolphins' Whistle Rate Across the Twelve Observation Sessions in the Follow-Up Phase
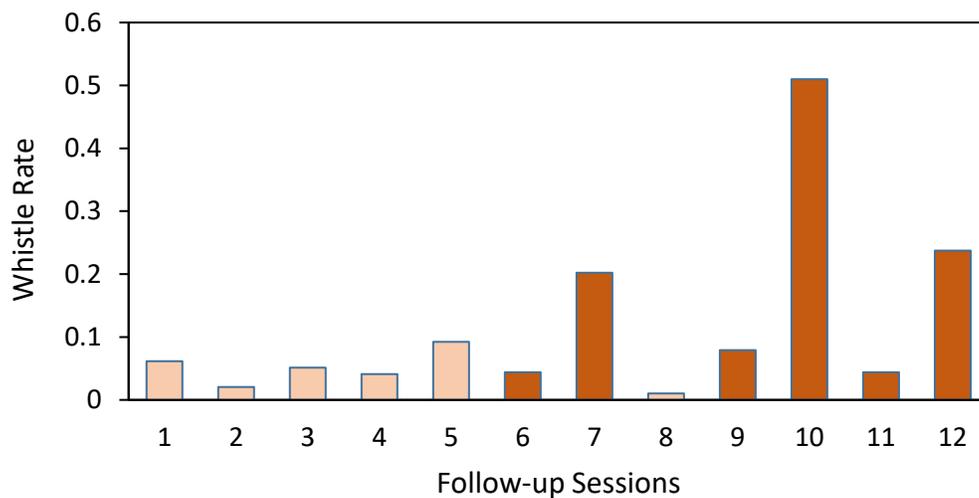
Note. Light tan bars represent sessions when the new dolphin was separate from the residents. Dark orange bars represent sessions when the new dolphin was free-swimming with the residents.

H3: Whistle Production by Phase—New Dolphin

As mentioned at the beginning of this section, three of the new dolphin's observations that occurred during the follow-up phase happened while she was free-swimming with the resident dolphins. In that situation, it was impossible to differentiate the whistles produced by the new dolphin from those produced by the residents. Therefore, the new dolphin's whistle rates collected during three of the resident dolphins' follow-up observations (when she was isolated from the residents) were incorporated as a substitute. With the substitutions, there was a significant association between the new dolphin's whistle production and phase, χ^2 ($df = 3$, $N = 217$) = 25.93, $p < .001$, Cramer's $V = .35$, representing a medium effect size (see Figure 9), supporting **H3**. Unfortunately,

Figure 9

Percentage of Intervals Containing a Whistle Produced by the New Dolphin Across

Phases
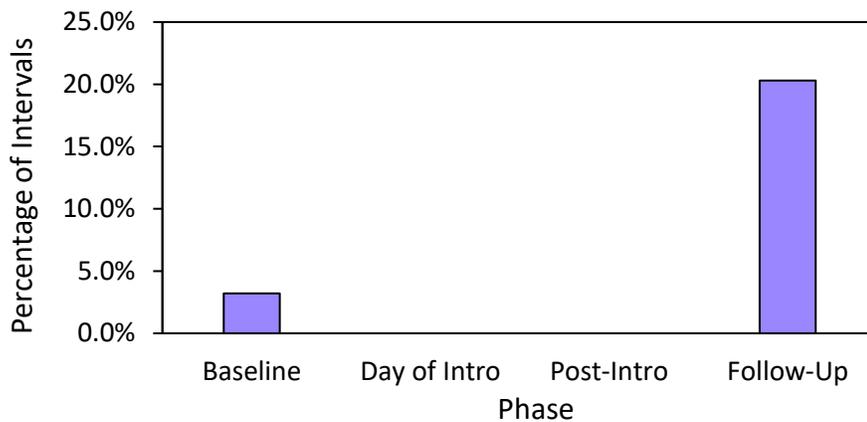
four of the cells (50%) had expected counts less than 5, violating one of the assumptions of the chi-square test (i.e., no more than 20% of the expected counts should be less than 5). While a Fisher's Exact Test is normally used for small expected frequencies in 2 x 2

tables, the preferred alternative to chi-square tests for larger contingency tables is the likelihood ratio statistic (Field, 2013). In this case, the likelihood ratio confirms the significant result found by the chi square test, Likelihood Ratio ($df = 3$) = 26.82, $p < .001$. This association remained significant even without the replacement sessions, Likelihood Ratio ($df = 3$) = 11.94, $p = .008$. The new dolphin produced the lowest proportion of whistles during the day of introduction and post-intro phases (0%), as she was silent throughout those observations, and the highest proportion of whistles during the follow-up phase (20.3%).

The new dolphin's whistle rate was also calculated for each of her behavioral observations. Her whistle rate was at its' minimum during the day of introduction and post introduction phases ($M = 0$) and at its' maximum during the follow-up phase ($M = 0.50$; see Figure 10). When analyzed by date of data collection, there were multiple days when the new dolphin was silent. Her highest mean whistle rate occurred on May 23rd ($M = 0.56$; see Figure 11).

Figure 10

New Dolphin's Mean Whistle Rate Across Phases
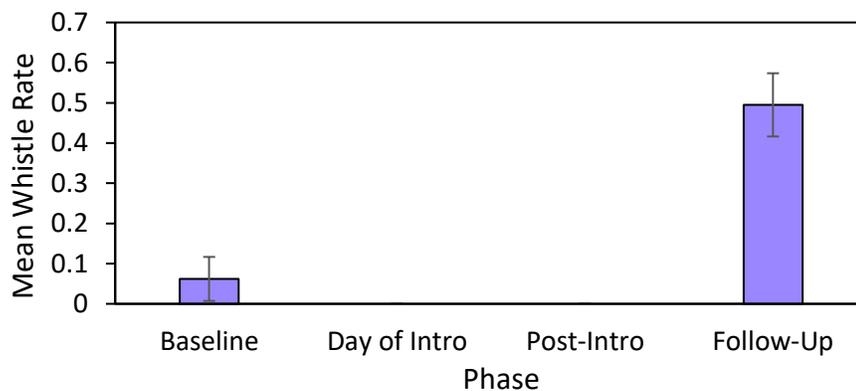
Note. Error bars represent 95% confidence intervals.

Figure 11

New Dolphin's Mean Whistle Rate by Date of Data Collection
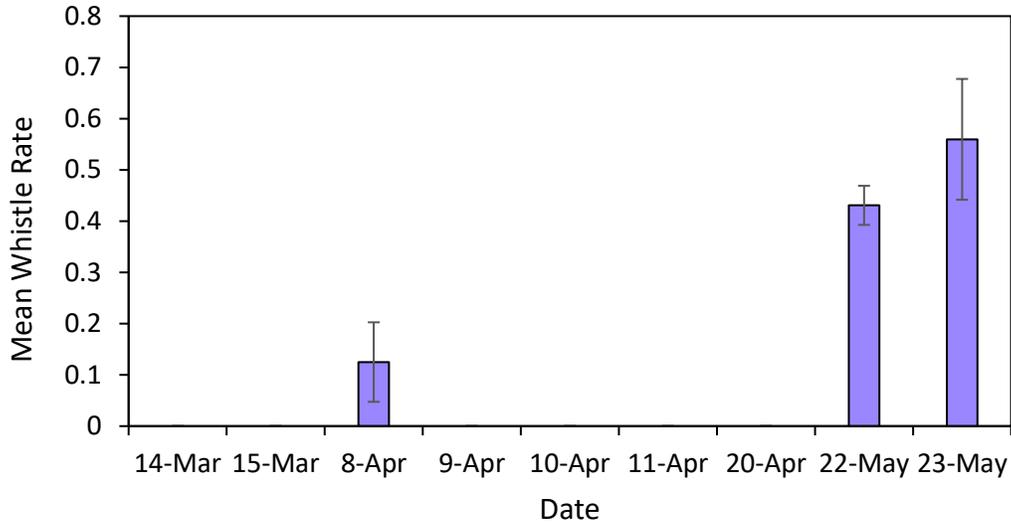
Note. The date of introduction is highlighted in green. Error bars represent 95% confidence intervals.

H4: Whistle Production as a Function of Social Behavior—Resident Dolphins

When collapsed across phases, the resident dolphins' social behaviors (prosocial and aggressive behaviors combined) were significantly related to their whistle production, χ^2 ($df = 1$, $N = 1109$) = 3.88, $p = .049$, $\varphi = .06$, providing support for **H4**. This association appears to be driven by the relationship between prosocial behaviors and whistle production (χ^2 ($df = 1$, $N = 1109$) = 4.28, $p = .038$, $\varphi = .06$) as opposed to the relationship between aggressive behavior and whistle production (χ^2 ($df = 1$, $N = 1109$) = 0.23, $p = .634$, $\varphi = .01$; see Figure 12).

Figure 12

Relationship Between Social Behaviors and Whistle Production Collapsed Across Phases
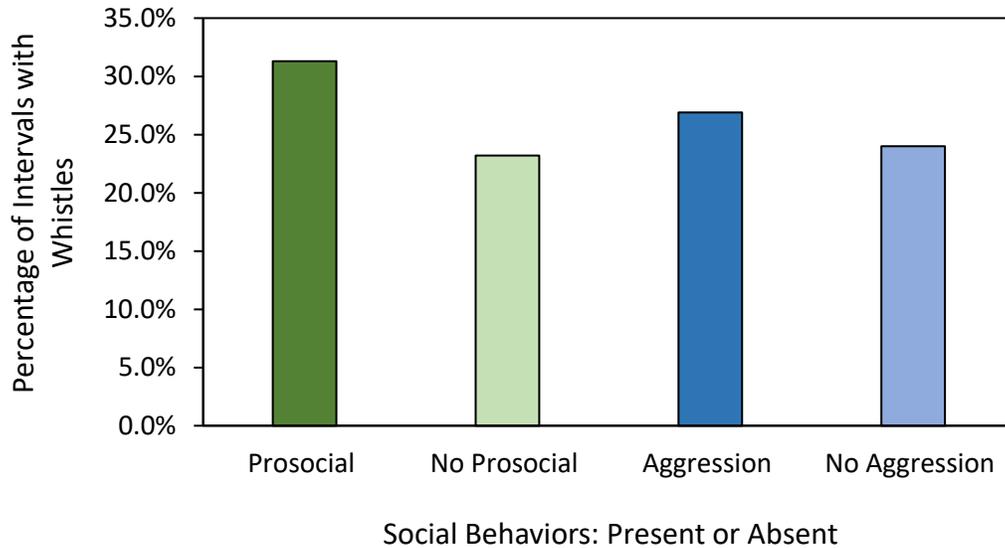
Note. The percentage of intervals containing both whistles and social behaviors (broken down into prosocial and aggression) are compared to intervals containing whistles with no social behavior for resident dolphins collapsed across phases.

While the relationship between the resident dolphins' social behaviors and their whistle production was significant when considering all the phases as a whole, the research question focused on if this relationship holds within each phase of the study.

Baseline

Within the baseline condition, the resident dolphins' social behaviors were significantly related to their whistle production, χ^2 ($df = 1$, $N = 348$) = 9.56, $p = .002$, φ = .17, providing further support for **H4**. Intervals containing social behaviors involving the focal dolphin ($n = 47$) also contained at least one whistle 36.2% of the time. Intervals without any social behavior observed ($n = 301$) contained at least one whistle 16.9% of

the time (see Figure 13 for graph of social behaviors x whistle production across all phases). During the baseline condition, the odds of the resident dolphins producing a whistle in the same interval as a social behavior were 2.78 times higher than the odds of the residents producing a whistle in an interval without a social behavior.

Figure 13

Relationship Between Social Behaviors and Whistle Production Across All Phases
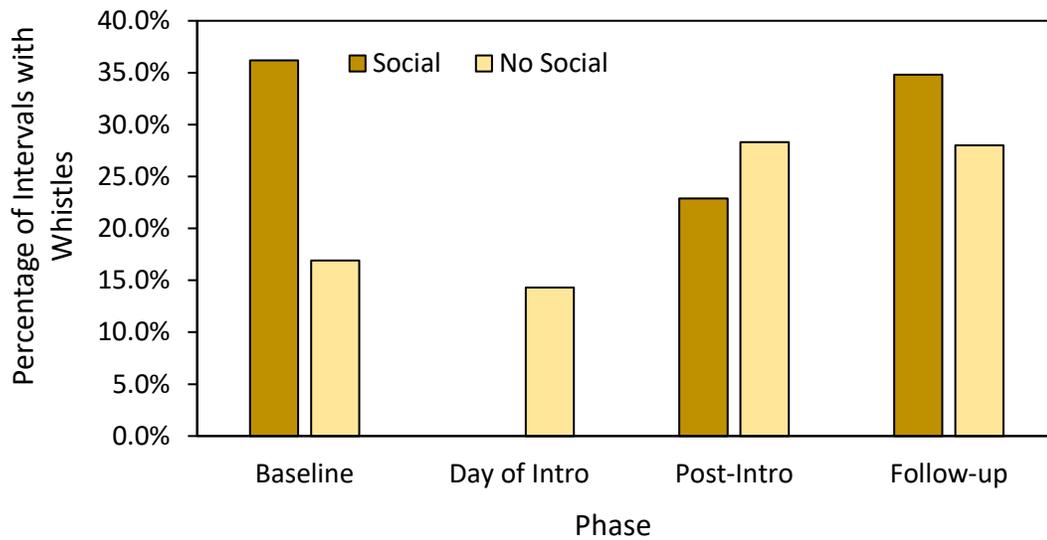
Note. The percentage of intervals containing both whistles and social behaviors are compared to intervals containing whistles with no social behavior for resident dolphins across all phases of the study.

To further decompose the relationship between social behaviors and whistle production during the baseline phase, prosocial and aggressive behaviors were analyzed separately. The resident dolphins' prosocial behaviors were significantly related to their whistle production, χ^2 ($df = 1$, $N = 347$) $= 5.78$, $p = .016$, $\varphi = .13$ (see Figure 14). Intervals with prosocial behaviors ($n = 38$) contained at least one whistle 34.2% of the

time, while intervals without prosocial behaviors ($n = 309$) contained at least one whistle 17.8% of the time. The odds of an interval containing a whistle were 2.3 times higher when the interval contained a prosocial behavior than when it did not.

The resident dolphins' aggressive behaviors were also significantly related to their whistle production, χ^2 ($df = 1$, $N = 348$) = 5.04, $p = .025$, $\varphi = .12$ (see Figure 14). The expected count of one of the cells was less than 5, violating one of the assumptions of the chi-square test, therefore Fisher's Exact Test was also used (Fisher's Exact Test = .036). Intervals with aggressive behaviors ($n = 14$) contained at least one whistle 42.9% of the time, while intervals without aggressive behaviors ($n = 334$) contained at least one whistle 18.6% of the time. The odds of whistle production was 3.29 times higher when the interval contained an aggressive behavior than when it did not.

Figure 14

Relationship Between Social Behaviors and Whistle Production During Baseline
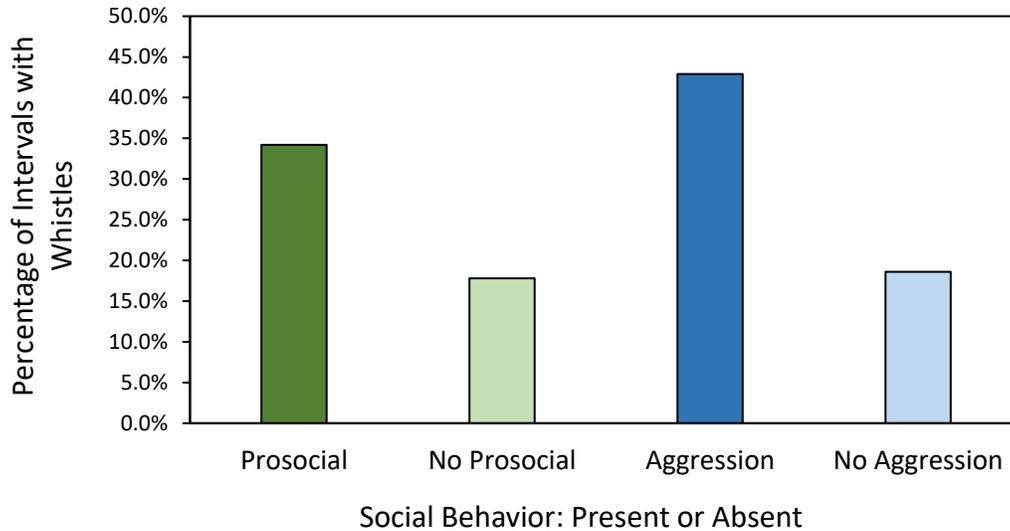
Note. The percentage of intervals containing both whistles and social behaviors (broken down into prosocial behaviors and aggression) are compared to intervals containing whistles with no social behavior for resident dolphins in the baseline phase.

Post-Introduction Phases

In contrast to the baseline phase, the resident dolphins' whistle production was not related to social behaviors for any of the post-introduction phases (day of introduction: χ^2 ($df = 1$, $N = 107$) = 1.48, $p = .224$, Fisher's Exact Test = 0.602; post-introduction: χ^2 ($df = 1$, $N = 324$) = 0.59, $p = .444$; follow-up: χ^2 ($df = 1$, $N = 330$) = 1.22, $p = .269$), patterns which do not support **H4**. Interestingly, during the day of introduction, the residents did not produce any whistles during the two aggressive intervals, and very few (if any) whistles during the prosocial intervals. There were 5 intervals with whistles (out of 14) eliminated due to the whistle producer being

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undeterminable. Two of those intervals also contained a prosocial behavior. Of the 7 remaining intervals containing prosocial behaviors, none of them cooccurred with whistle production.

H5: Whistle Production as a Function of Social Behavior—New Dolphin

Prosocial behaviors were impossible for the new dolphin during the baseline phase and highly unlikely during the subsequent phases due to her being physically separated from the resident dolphins. Prosocial behaviors thus only occurred during the follow-up phase in observation sessions where the new dolphin was free-swimming with the residents. Unfortunately, whistles could not be localized to her in that situation. Therefore, it was only possible to assess whether the new dolphin's prosocial behaviors related to the entire group's whistle production during those three free-swimming sessions. There was no association between the new dolphin's social behaviors and the group's whistle production, χ^2 ($df = 1$, $N = 44$) = 1.13, $p = .288$, Fisher's Exact Test = 0.314, supporting **H5**. Her total counts for aggressive behaviors throughout all phases of the study were too low to analyze ($n = 2$).

CHAPTER IV – DISCUSSION

The rough-toothed dolphins in the present study were observed over several months while a new conspecific was being integrated into a resident population. Patterns of acoustic and non-vocal behavior changed across the phases of the study for both the residents and the new dolphin, though changes were especially profound for the new dolphin. When first introduced to the residents, she was silent and stationary for prolonged periods of time, but as the months progressed, she became a socially active, vocal, and fully integrated member of the pod. Below I review specific results for each research question and consider whether the results support the stated hypotheses.

Social Behavior Across Phases

The first hypothesis **(H1)** focused on how often the resident dolphins were engaging in social behaviors throughout the phases of the introduction. Specifically, I predicted that the resident dolphins would engage in more social behaviors during the post-introduction phases than during baseline, before they were introduced to the new dolphin. The social behaviors of interest included both aggression and prosocial behaviors such as tactile contact and swimming in close proximity to another dolphin for an extended time. **H1** was partially supported by the results: when social behaviors were analyzed as a whole, there was an association with phase of the study, though the effect was small. Analyzed separately, aggressive behaviors showed a significant, but small, association with phase, while prosocial behaviors did not.

The resident dolphins' engaged in the lowest proportion of social behaviors during the day of introduction phase. This result may be a reflection of the anomalous activities occurring in the habitat that day. The new dolphin was visually and acoustically

introduced to the residents at approximately 8am on the day of introduction. This involved a large group of trainers carrying her past the residents and over to a small area of their enclosure, demarcated by a grated gate. Multiple trainers then entered the water to facilitate the new dolphin's safe entry into the habitat. After her initial introduction, large groups of trainers remained in and around the enclosure for the majority of the day. The situation was highly unusual as there are rarely that many familiar individuals around, and in, the habitat—and none of the residents were the focus of their attention. The residents' behavior throughout this time was marked interest in the unusual activity. Many of them spent long periods of time at the gate to the new dolphin's area of the enclosure, watching her and the trainers working with and comforting her. The resident dolphins appeared more interested in assessing what was happening in the new dolphin's area of the enclosure than interacting with each other on that particular day. This behavior was not entirely surprising as multiple reports describe the species as being highly curious (Kuczaj & Yeater, 2007; Lilley et al., 2018; Ritter, 2002).

Low rates of aggression during the initial introduction of a novel conspecific do not reflect the same patterns reported in early descriptions of dolphin introductions in human care settings. Many of early reports were characterized by high levels of aggression on the day of introduction (Caldwell & Caldwell, 1977; McBride, 1940). As in Broadway (2017), aggression was likely mitigated in the current study by the method of introduction: the new dolphin was initially physically separated from the residents, while visual and acoustic contact was possible. Only two instances of aggression were noted, both involving a resident dolphin slapping their chin on the surface of the water. Over the subsequent days, the resident dolphins were brought into the new dolphin's area

of the enclosure one-at-a-time during a feeding session, a highly controlled situation. By the 10th day after introduction, resident dolphins were spending periods of time, unsupervised, in the new dolphin's area of the habitat (one-at-a-time at first).

Throughout the study, only four instances of aggression involved the new dolphin. In three of these, the new individual was chased by a resident and in the fourth she made an aggressive movement (open mouth) toward the hydrophone. It is worth noting that some research suggests this open mouth behavior also occurs outside of aggressive contexts and may also indicate excitement or curiosity (Dudzinsiki, 1998; Lilley et al., 2018).

The classification of the three chases as aggression could also be called into question. McBride and Hebb (1948) reported that if a new dolphin was female, the dominant male in resident pods would commonly show a sexual interest in her, remaining near the gate to her area for hours at a time, with an erection, even before physical contact had been established. The perpetrator of two of the chases in current study was one male in particular, Ivan, who was observed engaging in similar behavior, spending prolonged periods of time at the gate to the new dolphin's area of the habitat, lifting his flukes at times, possibly posturing to her. After the new dolphin was free-swimming with the group, Ivan was one of the two dolphins most frequently observed swimming next to her, engaging in long periods of pectoral fin contact. In previous studies, Hanna (2016) noted that Ivan was involved in the dyad with the highest rates of association in that population and was one of only two dolphins that displayed any sexual behaviors, Caffrey (2013) mentioned that Ivan was one of four dolphins that engaged in any aggressive behavior, and Yeater et al. (2013) reported Ivan was the initiator of most the

chases and social behaviors throughout their observations. Therefore, the three chases in this study may have been sexual in nature as they involved two different males chasing the young female, with the main perpetrator, Ivan, appearing to be high on the dominance hierarchy and socially/sexually active within the pod.

By the last phase of the study the new dolphin was spending the majority of time free-swimming with the resident dolphins. Half of the behavioral observations on the resident dolphins throughout this phase occurred while the new dolphin had physical access to the residents, while the other half occurred while she was temporarily separated into her original area of the enclosure. As a whole, this was the phase where the highest proportion of social behaviors were observed, as predicted. Not only were more dolphins available for physical contact during half of the follow-up phase, affording resident's more opportunities for social interaction, one of those dolphins was an unfamiliar young female. The curious and social nature of the species suggests that the residents were likely interested in establishing a relationship with this new individual through prosocial behavior (Kuczaj & Yeater, 2007; Lilley et al., 2018).

An interesting difference was observed between the proportion of social behaviors that occurred between the two follow-up conditions: new dolphin alone vs. new dolphin free-swimming with the resident group. Prosocial behaviors showed a dramatic increase from the observations when the new dolphin was separate to the observations when she had physical access to the group. Aggression showed the opposite pattern, with much lower levels when the new dolphin was free-swimming with the residents. This difference provides additional evidence that despite high levels of aggression in the follow-up phase as a whole, the residents eagerly incorporated the new dolphin into the

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population with little to no indication of distress or discomfort when she was swimming

with them. The pattern also reflects how prosocial behaviors such as social swims and

tactile contact contribute to establishing and maintaining strong social bonds (e.g.,

Dudzinski & Ribic, 2017), and are thought to be especially important for rough-toothed

dolphin relationships (Hanna, 2016; Kuczaj & Yeater, 2007).

Whistle Production: Resident Dolphins

The second research question involved changes in the resident dolphins' whistle

production across the phases of the study. **H2** stated more whistles would be produced

during the post-introduction phases than baseline, as the residents were forming

relationships with the new dolphin. The resident dolphins' whistle production did change

across the phases, with the highest proportion of whistles being produced in the post-

introduction and follow-up phases. While that relationship supports **H2**, whistle

production actually declined on the day of introduction then rebounded to well above

baseline levels for the post-introduction and follow-up phases. While Broadway (2017)

reported similar results, low rates of whistle production on the day of the introduction

remain somewhat surprising since dolphins are known to exchange signature whistles

when encountering other dolphins in the wild (Quick & Janik, 2012). This may be

explained by the nature of the introduction (visual/acoustic vs. physical) and the

unfamiliarity of the new individual. Another possible explanation is that the dolphins

were so captivated by the unusual human activity, they refrained from producing whistles

in an effort to investigate.

The resident dolphins produced the highest proportion of whistles during the post-

introduction and follow-up phases, supporting **H2**. These findings fit with reports that

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whistles are social signals and increase during social situations, such as non-directional swimming (Quick & Janik, 2008) and excitement (Herman & Tavolga, 1980). Looking to the whistle rate by date of data collection, two large humps are evident. This is likely an artifact of there being only one observation a day included for those particular days. A high value on those observations had no chance of being attenuated by a more typical observation. On April 18th, the observation session occurred early in the morning, before any feeding sessions. The hydrophones had just been placed in the water and Ivan was especially focused on them during that time. He was extremely vocal, many of his whistles could be heard above water. The second large hump represents an observation session that occurred on July 24th. While observations were ideally made when there were no trainers interacting with the dolphins, this observation session was one of the exceptions. Half of the observation occurred while trainers were providing enrichment to the dolphins, which involved vocal and physical interactions from the side of the pool, but no training or primary reinforcement (i.e., fish). The majority of the whistling occurred during this enrichment session.

A post-hoc assessment of observation sessions within the follow-up phase showed a higher whistle rate in sessions where the new dolphin had physical access to the resident dolphins than sessions where she was physically isolated. Those results fit with the fact there was a higher proportion of social behaviors in those sessions. Perhaps it took a physical union to find results similar to Quick and Janik (2012), namely increased whistle production when dolphins meet in the wild.

Whistle Production: New Dolphin

The third hypothesis (**H3**) predicted the new dolphin's whistle production would be highest during the post-introduction phases. The relationship between the new dolphin's whistle production and the phase of the introduction was the strongest association found throughout the entire study. The proportion of intervals containing whistles produced by the new dolphin was by far the highest during the follow-up phase. Specifically, the new dolphin produced 4 whistles during her observations in the baseline phase, none during the day of introduction and post-introduction phase, and 23 during the follow-up phase—a pattern strongly supporting **H3**.

In addition to occurring when dolphins converge, high whistle rates have also been tied to stressful situations, such as when dolphins are isolated from their pod (Caldwell et al., 1990; Esch et al., 2009; Janik & Sayigh, 2013). At first glance, the current findings seem to suggest the new dolphin was not using her whistles in that manner, as she was silent on the day of introduction and shortly thereafter, but upon closer inspection, the results of the current project fit previous literature. Specifically, Caldwell et al. (1990) showed that bottlenose dolphins increase their whistle rate during mildly stressful events, but refrain from vocalizing when under higher levels of stress. Bowles and Anderson (2012) echoed this finding, stating that dolphins limit their vocal production when they perceive a threat as way to avoid detection. The new dolphin was likely experiencing quite a bit of fear and stress on the day of introduction and shortly thereafter as she had been completely isolated from all other animals since her rescue approximately six months before. The combination of being removed from a familiar setting (medical pool) and placed into a new enclosure where she could see and hear six

unfamiliar individuals was likely perceived as somewhat threatening and her silence was a natural fear response. Broadway (2017) observed Chance responding in a similar manner when he first encountered his new conspecifics.

After some months had passed (during the follow-up phase), the new dolphin in the current study was spending large amounts of time with the residents, frequently engaging in prosocial behaviors. During that time, the trainers would occasionally separate the new dolphin back into the small area of the enclosure she first became accustomed to. This was the only situation where the new dolphin's whistle rate could be calculated during that phase. Therefore, her high whistle rate during the follow-up phase was likely the result of her trying to maintain contact with her new pod while experiencing mild stress from the separation (Caldwell et al., 1990; Janik & Sayigh, 2013; Esch et al., 2009).

Relationship Between Whistle Production and Social Behavior

The fourth research question focused on a possible relationship between resident dolphins' social behaviors and their whistle production, and whether that may change across phases of the introduction. **H4** stated that social behaviors would be positively related to whistle production throughout all phases of the study since whistles are commonly reported as communicative, social signals (Cook et al., 2004; Janik & Sayigh 2013). The patterns observed were partially consistent with **H4**. When analyzed as a whole, there was a weak association between the resident dolphins' social behaviors and their whistle production. This appeared to be a result of the association between prosocial behaviors and whistle production, as the relationship between aggression and whistle production was negligible.

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Interestingly, when broken down by phase, the relationship between the resident dolphins' social behaviors and their whistle production only held true for the baseline condition. For that condition specifically, both prosocial and aggressive behaviors were found to have a weak association with whistle production, providing support for **H4**. Yet, the relationship disappeared in each of the other phases, a pattern inconsistent with **H4**. This unexpected result may be partially due to methodological constraints. Observations were conducted using a focal follow methodology which, by definition, only focuses on the behavior of one individual in the group. It is highly likely that social behaviors were occurring with individuals that were not being observed at the time, yet their whistles were being picked up by the hydrophones and included in the analysis. Karniski et al. (2015) outlined these issues by discussing differences in data collected via focal follows versus surveys. These differences can be attributed to where the observers attention is focused: on the group as a whole, or on a particular individual. Surveys can miss individual-level behavior and focal follows often fail to represent the behavior of all individuals in the group.

The fifth research question involved whether there was a relationship between the new dolphin's social behavior and her whistle production. Opportunities for prosocial behaviors were nonexistent during baseline due to the new dolphin's separate location, and very limited during the other phases when she was physically isolated from the residents. Therefore, the new dolphin's whistle production was predicted to change over time **(H3)**, as she became integrated with the residents, and not predicted to depend on her social behaviors **(H5).** Unsurprisingly, the new dolphin did not engage in any prosocial behaviors when she was physically isolated from the residents. The new

dolphin's only prosocial behaviors occurred when she was free-swimming with the residents during portions of the follow up phase, making it impossible to determine the whistle producer. Aggressive behaviors involving the new dolphin occurred to infrequently to analyze. Therefore, the only possible analysis including the new dolphin's social behaviors involved testing for an association between her social behaviors and the whistle production for the entire group during those few observation sessions where she had access to the residents. No association was found, providing support for **H5.**

Limitations and Future Directions

One of the major drawbacks to the current study involved the limited conditions under which the producer of the whistles could be accurately identified, a notoriously difficult problem (Lopez-Rivas & Bazua-Duran, 2010; Thomas et al., 2002). As previously discussed, whistles could only be localized to the new dolphin when she was physically separated from the residents. This did not pose a problem during the early phases of the study, but became more difficult to manage as the new dolphin fully integrated into the resident pod. During the final phase, the new dolphin had physical access to the residents for the majority of the day, so her whistles could not be differentiated from those produced by the residents. Most of the observations during the follow-up phase where the new dolphin was temporarily separated involved her taking part in a training session characterized by long periods of minimal interaction from the trainer. The trainer would come and go sporadically, moving away from her enclosure for several minutes or more at a time—sometimes visible, sometimes out-of-sight. While it is likely that some of the new dolphin's whistling in the follow-up phase was to maintain contact with the resident dolphins while she was isolated, broadcasting her location,

identity, and emotional state (e.g., Caldwell et al., 1990), she may have also been whistling in an attempt to regain the trainers' attention. While this situation was not ideal for collecting behavioral observations, there were no other opportunities for the observers to collect data on the new dolphin's whistle production during the follow-up phase.

One possible solution to this problem would be to attach a lightweight tag to each dolphin that was capable of either recording whistle production or illuminating a light when that dolphin was vocalizing. Either design theoretically allows the researcher to collect acoustic data for each individual, thus enabling whistle production to be accurately correlated to specific behaviors. While this idea is great in theory, past attempts have not been entirely successful. Tyack (1986, 1991) experienced obstacles with both methods involving the tag on one individual being activated when a second dolphin in close proximity was producing whistles, preventing accurate identification of the whistle producer. The dolphins vocal behavior also has been noted to change when they are wearing the recording equipment (Tyack, 1986). Therefore, the localization problem remains difficult to overcome.

An additional obstacle faced by the researchers involved the inability to record all of the residents' individual behaviors at one time, creating a difference in granularity between observations of vocal and non-vocal behavior. While social behaviors were recorded using a focal follow method, resulting in individual-level data, the resident dolphin's whistle production could only be collected for the entire group. This likely contributed to the nonsignificant results found when assessing the relationship between social behaviors and whistle production within three of the four phases of the current study. Extra cameras could help to overcome this problem on future projects. A drone

could potentially be used to capture overhead video of the entire population. The habitat also has several underwater windows that could potentially serve as future camera locations. High-resolution video footage from multiple angles would enable observers to record every instance of social behaviors occurring in the population throughout each observation, resulting in a more accurate interpretation of the relationship between social behaviors and whistle production.

A final limitation of this project is the question of generalizability. Does this introduction typify other introductions in captive rough-toothed dolphins? The question remains open partly because four of the seven dolphins in this study (including the new dolphin) have experienced some degree of hearing loss. It is possible that these particular dolphins are modifying their whistle production and non-vocal behaviors in some way as a result of that loss. Also, individual differences in age, sex, and personality may further serve to make the results of this study unique to this particular introduction. Comparisons to other populations of rough-toothed dolphins in human care are difficult as the second population in the northern hemisphere consists of two dolphins that were only rescued and rehabilitated last year (whom also are affected by hearing loss). Future work could include comparisons between the current population and the second population, if they happen to experience an introduction of a new conspecific.

There are several practical applications of these results if this introduction is assumed to be typical of other cetacean introductions in human care settings. The dramatic decrease in social behaviors on the day of introduction in the current project and Broadway (2017) may be seen as preferable to the highly aggressive behaviors that characterized early reports of dolphin introductions. One take-away from the similarities

between the current project and Broadway (2017) is that initial aggression can be greatly reduced by beginning with a visual and acoustic introduction. Physical contact happened gradually over time, during controlled training sessions when positive, calm interactions could be immediately reinforced. While the resident dolphins' aggressive behaviors did rebound to above baseline levels in the current project's follow-up phase, most of these were subtle chin slaps, open mouth behaviors, and potentially sexual or playful chases that did not involve the new individual and occurred while she was physically isolated in one section of the habitat.

The current project also highlights how whistle production of a new individual may be a useful metric of his/her perceived bond with the resident pod. The new dolphin in the current project only increased her whistle production when she was physically isolated from the residents after she had spent a considerable amount of time free-swimming with them. Animal care workers may be able to assess a new individual's whistle production when isolated from the pod. If a new dolphin is showing especially high whistle rates in that situation, it may be a positive sign that he or she has begun to form bonds of attachment with the residents, and is motivated to maintain acoustic contact with them when physical contact is not possible.

Conclusions

The aim of this project was to describe how rough-toothed dolphins use social behaviors and whistle production to navigate the integration of a new dolphin into a resident pod. While whistle production and social behaviors were at their lowest on the day of introduction, this is likely the result of the initial introduction being purely visual/acoustic rather than physical. Social behaviors and whistle production rebounded

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and exceeded baseline levels during the final phase of the study (especially for the new dolphin), when observations included the new dolphin free-swimming with the residents. This pattern was suggestive that the dolphins in this study were utilizing social behaviors, especially social swimming and tactile contact, and whistle production to establish and maintain new social bonds. This project may inform multiple areas of study including how rough-toothed dolphins use vocal and non-vocal behavior to navigate the formation of new relationships, impacts of the introduction of a conspecific on both the resident population and the new individual being integrated, and husbandry management procedures involving future introductions.

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