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Signature Whistle Production during a Bottlenose Dolphin Group Integration

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SIGNATURE WHISTLE PRODUCTION DURING A BOTTLENOSE DOLPHIN

GROUP INTEGRATION

by

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December2017

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ABSTRACT

SIGNATURE WHISTLE PRODUCTION DURING A BOTTLENOSE DOLPHIN

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Bottlenose dolphins are an important species of interest because they possess a

variety of abilities that are relatively rare in the animal kingdom, one being complex

acoustic communication. Signature whistles - distinctive calls that are unique for each

individual – are one of the most studied call types, but we know little about how these

calls are used in various contexts, such as during an introduction. Looking at the socio-

behavioral context in which signature whistles are used is likely the best way of learning

how these whistles are used in a particular context (Caldwell, Caldwell, & Tyack, 1990).

For this project, the behavior and vocalizations of dolphins that were being introduced for

the first time were analyzed to assess how signature whistle production and behavior

changed after introduction. The new individual, a juvenile male, was kept physically, but

not visually and acoustically, separated during the introduction. Signature whistle

production for the new dolphin declined steeply on the day of introduction, increased the

following week, and almost fully recovered over a month later. Overall, he produced

approximately three times more signature whistles than the other dolphins. The resident

female showed interest in the new individual following the initial introduction, and her

signature whistle production increased after the introduction. The resident adult male

showed little interest in the newcomer and his signature whistle production increased

slightly. Following introduction, there were only slight changes in the behavior of

resident group members, which included increased circle swimming and object play. Circle swimming also increased significantly for the new individual. There were no differences in social behavior and no agonistic behaviors were observed. The new dolphin's decrease in signature whistling on the day of introduction was unexpected but may be due to individual differences in response to stress. In some ways, these findings are inconsistent with the few reports of typical bottlenose dolphin behavior during an introduction. Information from additional introductions will be needed to determine if the patterns of signature whistle usage and behavior seen here are typical of the range of behaviors exhibited in this context.

ACKNOWLEDGMENTS

DEDICATION

I would like to dedicate this work to my mom, dad, and grandparents for their endless support throughout this journey and to my husband for following me as I chased my dreams. To date, the completion of my Ph.D. is my second greatest accomplishment, my greatest accomplishment being my daughter, Ava. In the end, my family, extended family, and friends all helped make this possible. It takes a village and I have the best.

I would also like to thank my committee for their influence and guidance over the course of my time at USM. I would like to thank Dr. Elena Stepanova for agreeing to be on my committee and also for her guidance during a very difficult semester. I would like to thank Dr. Hans Stadthagen for his mentorship and for passing on a very important piece of advice concerning a dissertation or thesis, "Just finish it and turn it in. It doesn't have to be perfect." I would like to thank Dr. Danielle Greenhow for making a fantasy a reality when I was able to assist with data collection for the Sarasota Wild Dolphin Project. And finally, I want to thank my friend, advisor, and mentor Dr. Heidi Lyn for altering my path in life. Without her, I would not have met the long list of amazing people that I have come to know in the last five years and would not have had the unbelievable experiences that I have had and will experience in the years to come.

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CHAPTER I - INTRODUCTION

The origin of human language continues to intrigue researchers and the general

public alike, due to the fact that it is one of the only "uniquely human" cognitive features

that has yet to be discovered to naturally occur in any animal species (Hauser, Chomsky,

& Fitch, 2002). Comparative research into the evolution of language offers a broad

avenue of investigation that hopes to shed light on how animal communication evolved

into language (Fitch, 2005; Shettleworth, 2012). One approach to studying the evolution

of language mirrors that of cognitive research in general. That is to identify the

mechanisms that are assumed to be key components of language and investigate these

components comparatively across species (Shettleworth, 2012). Aspects of language such

as vocal learning and referential labeling increase the complexity of a communication

system (Janik, 2009, 2013; Pepperberg, 2007). Complex communication systems have

been observed in a variety of species, including bees (Frisch, 1967), vervet monkeys

(Seyfarth, Cheney, & Marler, 1980), and birds (Doupe & Kuhl, 1999), but the degree to

which non-human species possess various aspects of language remains unclear (Hauser et

al., 2002). Primates have been an important species of comparison due to their close

evolutionary ties with humans, but they lack a complex vocal communication system

(Janik, 2009). Very few species possess extensive, flexible, vocal communication

systems as these features seem limited to humans, dolphins, and some bird species (Janik,

2009). Dolphins offer an interesting avenue for investigation because they possess a

unique combination of traits that is rare in the animal kingdom: a flexible communication

system that is influenced by vocal learning (Janik & Sayigh, 2013). Currently, there is

one major limiting factor in comparing dolphin communication to the communication

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systems of other animals. That is, we do not know the function of the vast majority of dolphin sounds (Luís, Couchinho, & dos Santos, 2015).

Although all delphinids vocalize, the bottlenose dolphin (*Tursiops spp.*) has been the focus of the majority of studies on dolphin communication due to their abundance in marine parks (Defran & Pryor, 1980; Herman, 2006; Janik & Slater, 1997; Williamson, Gales, & Lister, 1990) and the complexity of their vocal repertoire (Janik, 2009; McCowan, Hanser, & Doyle, 1999). As a result, we know more about bottlenose dolphins than any other delphinid species (Jaakkola, 2012). This being said, we know relatively little about the cognitive and communicative abilities of these animals (Jaakkola, 2012; Janik, 2014) – particularly when compared to what we know about non-human primates.

Cognitive research with animals and young children is difficult due to the limited ability to communicate with the subject; therefore, cognitive abilities are often assessed by interpreting behavior. Cues such as vocalizations and physical interaction are important to the interpretation of behavior for many species, specifically with regard to social behavior (Dawkins, 1998; Seyfarth et al., 1980). Using both physical behavior and communicative cues can accelerate cognitive studies by providing additional contextual information. Unfortunately, with research studies involving dolphins, it is not always possible to observe these cues. Descriptions of physical behavior are often limited to surface behaviors, and vocalizations are largely ignored in behavioral studies due to the difficulty of recording and localizing the source of sound underwater (Connor & Smolker, 2009; Janik, 2000b, 2009; Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010). In addition, dolphin vocalizations have proven difficult to decode so the meaning behind

most vocalizations remains almost entirely unknown (Luís et al., 2015). Deciphering the meaning of dolphin vocalizations would allow us a new window into the communicative processes that underlie their daily lives and may aid our ability to assess their cognitive abilities.

Possible Origins of Delphinid Communication and Cognition

It has been hypothesized that the development of a vocal communication system in dolphins may have been due to their underwater environment which favors the propagation of auditory signals over visual cues (Janik, 2009; Janik & Slater, 1997, 2000; Sayigh, Esch, Wells, & Janik, 2007). The auditory sensory system is particularly important for dolphins because sight is not reliable over large distances or under diminished lighting (night or at depth), and can change depending on the turbidity of the water (Janik, 2013, 2014; Tyack & Sayigh, 1997). In addition, sound travels farther in water allowing animals to remain in contact over large distances (Janik, 2000a; Quick & Janik, 2008). Vocal communication would be extremely important under these limiting environmental conditions (Janik, 2014; Janik & Sayigh, 2013; Tyack & Sayigh, 1997). Coupled with environmental pressures to communicate vocally, social pressures may have led to more advanced cognitive and communicative abilities in some dolphin species (Bruck, 2013; Herman, 2006; Herman & Tavolga, 1980; Janik, 2013; Marino, 2002; Smolker, Mann, & Smuts, 1993). A high degree of sociality has been identified as one factor that is present across species that possess complex communication systems (Freeberg, Dunbar, & Ord, 2012). These systems include features such as flexible signaling and the use of individually distinctive signaling mechanisms (Balsby & Bradbury, 2009; Freeberg et al., 2012; Janik, Sayigh, & Wells, 2006; Wanker, Sugama,

& Prinage, 2005). It has also been hypothesized that living in more social environments increases information processing abilities because it adds a layer of complexity that individuals in non-social environments do not have to deal with (Byrne & Whiten, 1988; Freeberg et al., 2012; Humphrey, 1976; Jolly, 1966). Individuals must be able to recognize others, remember the past actions of others, and predict future behavior (De Waal, 1982; Freeberg et al., 2012). They must also calculate and decide to act in their own immediate self-interest or act against their self-interests in order to gain clout among group members (Byrne, 1999; Byrne & Whiten, 1988; Freeberg et al., 2012). These social pressures are hypothesized to act on populations to advance cognitive abilities such as memory (Bruck, 2013).

Bottlenose Dolphin Society

Among delphinids and other odontocetes, the use of whistling as a means of communication is not universal; the Heaviside dolphin (*Cephalorhynchus heavisidii*) for example, does not whistle (Herman & Tavolga, 1980; Oswald, Rankin, & Barlow, 2008). Several factors have been suggested to have contributed to the loss of whistling, however, group size and predation are generally believed to be a primary contributing factor with large group size selecting for whistling and predation selecting against it (Morisaka & Connor, 2007; Oswald et al., 2008).

Most of what we know about bottlenose dolphin society comes from long-term field studies (Lusseau, 2003). Two of the longest running projects are located in Sarasota Bay, Florida (beginning 1970 - Wells, Scott, & Irvine, 1987) and Shark Bay, Australia (beginning 1985 - Connor & Smolker, 1985; Smolker, Richards, Connor, & Pepper, 1992). Both research sites are enclosed or semi-enclosed, shallow, sheltered areas with

warm waters (Scott, Wells, & Irvine, 1990; Smolker et al., 1992). Dolphins also inhabit deeper offshore waters and are found throughout tropical and temperate waters, thus what is typical in Sarasota Bay or Shark Bay may not be the norm for bottlenose dolphins that inhabit different ecological environments (Connor, 2007; Lusseau et al., 2003; Smolker et al., 1992). However, research from these sites can be used to demonstrate inclinations and develop inferences regarding general capacities for bottlenose dolphin behavior and cognition (Connor, 2007).

Bottlenose dolphins live in fission-fusion societies (Connor, Wells, Mann, & Read, 2000) and maintain long-term bonds with other individuals (Connor, 2007). Offspring typically remain with their mothers for between three and five years, which is a relatively long time in comparison to many other species (Connor & Mann, 2006; Connor et al., 2000; Harley, Fellner, & Stamper, 2010; Herman, 2006; Jaakkola, 2012; Tyack, 1986a). Both males and females can maintain large overlapping territories and individuals may be highly or only moderately social depending on factors such as their preferred foraging style (Connor & Mann, 2006).

Maintaining social relationships is an important aspect of life and offers an effective strategy for protection from predators, cooperative foraging, and mating (Connor, 2007; Lusseau et al., 2003). Most associations are brief, more akin to acquaintances, but individuals can maintain long-term relationships and remember individuals from the past for at least 20 years, if not more (Bruck, 2013; Connor, 2007; Lusseau et al., 2003). Females are known to associate with their adult offspring, as well as non-related adult females for many years and, males, at least in some areas, form life-

long alliances with other males for the primary purposes of securing mates (Connor et al., 2000).

<center>Bottlenose Dolphin Cognition</center>

The dolphin brain is highly encephalized compared to other odontocetes (Marino, 1998). Dolphins have the second highest encephalization quotient (EQ) – brain to body size ratio in comparison to other similarly sized mammals – following humans (Marino, 1998). Based on the studies that have been conducted, the cognitive abilities of dolphins are thought to be similar to that of great apes (Jaakkola, 2012). A few of the more unique cognitive abilities of dolphins will be highlighted.

Dolphins have the ability to reference and interpret references to objects both gesturally and acoustically. They can correctly interpret the pointing gestures of humans, follow eye gaze (Pack & Herman, 2004, 2007; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001), and use body position (Xitco, Gory, & Kuczaj II, 2004) and possibly echolocation (Gregg, Dudzinski, & Smith, 2007) to point to objects, an action that can potentially allow them to share information with others. They have also demonstrated the ability to reference objects acoustically through the use of vocal labels (Harley, 2008; Herman, Richards, & Wolz, 1984; Reiss & McCowan, 1993; Richards et al., 1984) and to use those labels to refer to objects that are not present (Herman & Forestell, 1985). Imitation is another area where dolphins excel. They can reproduce sounds vocally and imitate the motor movements of other dolphins and humans even though humans possess a body plan that differs dramatically from their own (Bauer & Johnson, 1994; Caldwell & Caldwell, 1972; Herman, 2002; Herman, Pack, & Morrel-Samuels, 1993; Jaakkola, Guarino, & Rodriguez, 2010; Janik, 2000b; Reiss & McCowan, 1993; Richards, Wolz, &

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Herman, 1984; Tyack, 1986b). They are also one of the few animals that have been successfully taught to understand and use human-generated symbolic communication systems (Herman, Richards, & Wolz, 1984). These are only a few of the more impressive cognitive abilities that have been investigated. Some other interesting areas of research that seem promising but have yet to be supported by solid empirical evidence include self-recognition, metacognition, and tool use.

Bottlenose Dolphin Vocalization

There are three main types of dolphin vocalizations: whistles, clicks, and burst-pulse sounds (Janik, 2009). Dolphin vocalizations can be characterized using several parameters including minimum and maximum frequency, duration, and contour, which is the "pattern of the frequency changes over time" (Sayigh & Janik, 2010). Whistles are frequency-modulated, narrow-band, tonal sounds that are used for communication (Janik, 2009). Whistles have a maximum frequency up to around 30 kHz (Janik, 2009) and are greater than 100 ms in duration (Lilly & Miller, 1961). Echolocation clicks are much shorter in duration, have a higher maximum frequency, and are thought to be associated with both echolocation and communication (Janik, 2009). Pulse sounds are a series of rapid clicks that usually have an interclick interval of less than 10 ms (Lammers, Au, Aubauer, & Nachtigall, 2004) and are typically associated with aggressive or excited behavioral states (Branstetter, Moore, Finneran, Tormey, & Aihara, 2012).

The understanding of dolphin vocal communication has not progressed as quickly as this same research with terrestrial species, such as primates, due to the difficulty of detecting and interpreting vocal activity and behavior underwater (Janik, 2009). Knowing which individual dolphin is vocalizing underwater is difficult to determine and

this knowledge is necessary when determining the function of a dolphin's vocalizations in relation to specific situations (Tyack, 1986b). To further complicate detection, dolphins can produce two separate sounds simultaneously making it appear as though multiple individuals are vocalizing (Janik, 2009). The development of passive acoustic localization which uses the timing of audio signals from multiple audio recordings to estimate the position of the sound source, has helped to overcome some of these issues (Janik, 2009; Janik, Parijs, & Thompson, 2000; Quick, Rendell, & Janik, 2008). More progress has been made regarding localization of echolocation clicks because clicks are short-duration, high-energy sounds that typically have a well-defined onset and are directional in nature. Localization of whistles is more difficult because whistles generally contain less energy and the onset of the sound may not be uniform across hydrophone channels. Whistles are also longer in duration and, if there is not a high degree of frequency modulation, localization may be difficult. These are some of the reasons why the meaning of the majority of dolphin vocalizations remains unclear (Janik, 2009).

<div align="center">Signature Whistles</div>

The most prominent finding regarding dolphin social communication was the discovery of signature whistles (Janik & Sayigh, 2013). Caldwell & Caldwell, (1965), noticed that when dolphins were in stressful situations, such as isolation, they tended to use one predominant, highly stereotypic whistle and that, unlike alarm or cohesion calls of other species, this whistle was unique for each individual. These unique calls were termed 'signature whistles'. From these observations the signature whistle hypothesis was formed – the signature whistle of an individual is unique and is the predominant whistle used when a dolphin is in isolation (Caldwell & Caldwell, 1965). These whistles

function primarily as cohesion calls to reunite group members (Janik & Slater, 1998), such as a mother and calf after a period of separation (Smolker et al., 1993). Signature whistles have since been defined as "a learned, individually distinctive whistle type in a dolphin's repertoire that broadcasts the identity of the whistle owner" (Janik & Sayigh, 2013, p. 482).

Individually distinctive calls are extremely rare in the animal kingdom and this ability has only been observed in humans, dolphins, and some parrot species (Balsby & Bradbury, 2009; Balsby & Scarl, 2008; Janik et al., 2006; Wanker et al., 2005). Identity information contained in signature whistles is encoded in the shape of the frequency contours of the whistle (Janik et al., 2006) and not in other features such as voice cues (Sayigh, Wells, & Janik, 2017). However, one other feature has been identified as a hallmark that can be used to reliably identify signature whistles; that is, these whistles are typically produced together in an uninterrupted series, also known as a bout, with an interwhistle interval of 10 seconds or less (Janik, King, Sayigh, & Wells, 2013). Approximately 90% - 100% of whistles produced in isolation are signature whistles (Caldwell et al., 1990; Janik & Sayigh, 2013; Janik & Slater, 1998; Sayigh et al., 2007), but signature whistles make up only 32-52% of whistles emitted by wild free-swimming dolphins under non-threatening conditions (Cook, Sayigh, Blum, & Wells, 2004; Watwood, Owen, Tyack, & Wells, 2005); although, higher rates, up to 70%, have been reported (Buckstaff, 2004).

Although the existence of signature whistles has been criticized in the past (McCowan & Reiss, 2001), these whistles have been found in many studies and across many delphinid species (Caldwell & Caldwell, 1965, 1968, 1971; Caldwell, Caldwell, &

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Miller, 1973; Gridley et al., 2014; Janik & Slater, 1998; Janik, Todt, & Dehnhardt, 1994; Sayigh et al., 2007; Sayigh, Tyack, Wells, & Scott, 1990; Sayigh, Tyack, Wells, Scott, & Irvine, 1995; van Parijs & Corkeron, 2001; Watwood, Tyack, & Wells, 2004). Caldwell et al. (1990) noted that in some rare cases, in approximately 8% of 126 dolphins studied, signature whistles were not observed or were presented in abnormal variations. These exceptions and the variable nature of the whistle may have contributed to the controversy surrounding the signature whistle hypothesis (Caldwell et al., 1990). The same signature whistle can be produced many ways often varying in characteristics such as duration, start and end frequency, and the number and duration of intervals between repeating whistle patterns, also known as loops (see Janik et al., 1994). It is hypothesized that these variations may contain additional information other than identity (Caldwell et al., 1990; Esch, Sayigh, Blum, & Wells, 2009; Janik et al., 1994; Tyack & Sayigh, 1997). For example, increases in the maximum frequency, the number of loops, and the rate of whistle production may be indicative of stress (Esch, Sayigh, Blum, et al., 2009).

Signature Whistle Development and Stability

The unique features of a calf's signature whistle appear during the first three months to two years of life (Caldwell & Caldwell, 1979). The development of the signature whistle is influenced by environmental sounds, including the signature whistles of other dolphins (Fripp et al., 2005; Richards et al., 1984; Sayigh et al., 1990; Tyack & Sayigh, 1997). Although findings are limited to the length of ongoing long-term studies, most dolphins, especially females, continue to use the same signature whistle over many years and possibly throughout their entire lives (Janik & Sayigh, 2013; Sayigh et al., 2007, 1990; Tyack & Sayigh, 1997; Watwood et al., 2005). However, there have been

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cases where signature whistles change over time, for example, with young animals

(Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997) or with close social acquaintances,

specifically male pair bonds (Smolker & Pepper, 1999; Watwood et al., 2004).

<center>Signature Whistle Copying</center>

Vocal copying is a form of vocal mimicry where one individual produces a

vocalization that is the same, or nearly the same as a sound produced by another

individual. Whistle matching is a term used to describe vocal copying that occurs within

a short time frame of up to a few seconds (Janik, 2000b, 2009). Although rare (Janik &

Sayigh, 2013), matching of signature whistles has been recorded in captive (Agafonov &

Panova, 2012; Janik & Slater, 1998; King, Harley, & Janik, 2014; Nakahara & Miyazaki,

2011; Tyack, 1986b) and wild populations (Janik, 2000b; King & Janik, 2013; King,

Sayigh, Wells, Fellner, & Janik, 2013; Sayigh et al., 1990; Tyack, 1993). Matching

interactions are typically observed in specific contexts but the meaning of this mimicry is

still unclear (Janik, 2009; Janik & Sayigh, 2013).

Signature whistle matching is a rare, affiliative signal that has only been reported

to occur between dolphins that associate frequently (King et al., 2014, 2013; Nakahara &

Miyazaki, 2011; Quick & Janik, 2012). This includes related individuals, such as a

mother and calf, and non-related individuals, such as male pair bonds (King et al., 2013).

Signature whistle matches are similar but not exact replicas of the owner's whistle (King

et al., 2013; Tyack, 1991) which may allow the copied whistle to serve a different

function than when the whistle is produced by its owner (Janik & Sayigh, 2013). It has

long been hypothesized that signature whistle matches may function to address, refer to,

or locate other individuals (Connor, 2007; Janik, 1995, 2009; Janik & Sayigh, 2013; King

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et al., 2014; King & Janik, 2013; Quick & Janik, 2012; Tyack, 1986b; Watwood et al., 2005). In addition, the matching of a signature whistle, in the context of a reply, may be a signal to confirm that a message produced by another individual has been received (Janik & Sayigh, 2013). There is evidence suggesting that dolphins do address one another in this way. In a playback study with wild free-swimming dolphins, King & Janik (2013) demonstrated that dolphins respond to hearing a copy of their signature whistle by calling out with the same whistle. In a similar study with captive dolphins, King et al. (2014) showed that dolphins respond to signature whistle matching by replying to the match.

Dolphins have the ability to reference and interpret references to objects both gesturally (Gregg et al., 2007; Pack & Herman, 2007; Xitco et al., 2004) and vocally (Harley, 2008; Herman et al., 1984; Reiss & McCowan, 1993; Richards et al., 1984), so it is plausible that they may also use signature whistles as a label for individuals. They also have the ability to use labels to refer to objects that are not present (Herman & Forestell, 1985), so it is possible that they may also use signature whistles to refer to individuals that are not present. Watwood et al. (2005) found that wild dolphins seemed to produce whistles that were extremely similar to the signature whistle of a conspecific that was not present at that time of the recording, which suggests that the dolphins may have been trying to locate individuals or were referring to individuals that were not present (Janik & Sayigh, 2013). This finding is intriguing but unprecedented.

In captivity, the function of signature whistle matching may not be exactly the same as it is in the natural environment, as captive dolphins generally remain in close proximity to one another due to the limitations of their enclosures, and group sizes are typically small; thus a cohesion call to locate or identify group members may be

inessential in captive settings (Agafonov & Panova, 2012). However, whistle matching in these situations may serve a different purpose. One such function could be related to maintaining social dominance. For example, in a captive setting, Agafonov & Panova (2012) found the highest rates of whistle matching for dominant individuals which copied the whistles of dolphins with a lower social standing.

<center>Dolphin Group Integrations</center>

Detailed information documenting dolphin introductions is lacking in the literature and the information that is available is mostly anecdotal in nature. These consist mainly of early accounts of the behavior of dolphins in marine parks from the 1940's and 50's (ex. Caldwell & Caldwell, 1977; McBride, 1940; McBride & Hebb, 1948) and then some additional descriptions provided as background information in studies focusing on other topics such as dominance hierarchies (ex. Samuels & Gifford, 1997). These reports often provide a brief description of the sex, age, and history of the dolphins that were involved in the introduction and report notable affiliative or agonistic events that took place following the introduction. A more detailed quantitative study monitored the social behavior of two groups of rough-tooth dolphins (*Steno bredanensis*) that were integrated to form one large group, but the dominance hierarchy that resulted did not fit with what is typically reported for bottlenose dolphins, indicating that there may be differences in the dominance relations of these two species (Yeater, Miller, Caffery, & Kuczaj II, 2013).

Although there are endless combinations of the age, sex, number of individuals, and personalities that can be involved in a bottlenose dolphin introduction, some responses may be typical in certain situations. For example, McBride & Hebb (1948) reported that a new female being introduced to adult males was courted immediately

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following physical introduction. The same was true for two adult males that were introduced together to a resident adult female (McBride, 1940). When the new animal and resident animals are the same sex and nearly equally matched in size, some interactions may be agonistic until a dominance hierarchy is established (Caldwell & Caldwell, 1977; Samuels & Gifford, 1997). For example, Samuels and Gifford (1997) describe the introduction of two females, aged 13+ and 15+ years, to a group of two resident females aged 12 and 30+ years. The resident females allied themselves against the new females with the most aggression occurring between the oldest female from each group. Introductions of younger, smaller animals were typically met with aggression by older, larger residents, sometimes resulting in death (McBride, 1940; McBride & Hebb, 1948). This was true whether the dominant resident animal was male or female. For example, McBride (1940) reported that when two smaller dolphins, a male and a female, were physically introduced to an adult female with her calf, the adult female harassed the newcomers almost continuously until they died four weeks later. In contrast to these accounts of behavioral responses, vocal responses to introduction are almost completely absent, with no reports at all of signature whistle production in this context.

<div align="center">Project Overview</div>

The purpose of this study is to examine the production of bottlenose dolphin signature whistles during the integration of a new individual into an existing social group. Because very little is known about the use of signature whistles in this context, the data presented here are a largely exploratory analysis of a dolphin introduction that occurred in 2012. Due to the exploratory nature of the study, this project includes a series of questions that help to characterize dolphin vocalizations, specifically signature whistles,

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in this context. The findings from this study will allow comparisons to be made to other situations where a new individual is added to an existing group. The questions and hypotheses for this study are as follows:

Question 1: Does the pattern of combined whistle production increase after the new dolphin is introduced to the existing group?

There is little information on whistle production in this context. However, it is expected that whistle production will increase after the new dolphin is introduced to the existing group.

Hypothesis: More whistles will be produced after the new dolphin is introduced to the existing group.

Question 2: Does the pattern of combined signature whistle production increase after the new dolphin is introduced to the existing group?

Again, there is little information on the use of signature whistles in this context. However, it is expected that signature whistle production will increase after a new dolphin is introduced to the existing group.

Hypothesis: More signature whistles will be produced after the new dolphin is introduced to the existing group.

Question 3: After introduction, which dolphin's signature whistle will be produced most often?

Stress and isolation are both factors that have been found to increase the rate of signature whistle production (Caldwell & Caldwell, 1965). Therefore, it is expected that whistle production of the new individual's signature whistle to be higher than that of the group members because the new individual will still be

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semi-isolated from the other dolphins. In addition, the new individual will likely be experiencing more stress than the others will because he will be in a completely new environment. The individuals in the existing group should be less stressed, as they were not removed from their environment and their established group would remain intact the entire time. As a result, it is expected that their whistles will be produced less often.

Hypothesis: After introduction, the new dolphin's signature whistle will be produced more often than the group's signature whistles.

Question 4: Does signature whistle matching occur when a new dolphin is integrated into the existing group?

Based on previous findings (King et al., 2013), it is unlikely that whistle matching will occur among dolphins that are unfamiliar with one another, therefore, mimicry of signature whistles is not expected.

Hypothesis: Mimicry of signature whistles will not be observed during the introduction or post-introduction periods.

Question 5: Does the behavioral repertoire of the new dolphin change after he is introduced to the group?

Because dolphins are highly social animals (Connor, 2007) and the new dolphin will have been in isolation for several months prior to the introduction, it is expected that there will be an increase in social activity exhibited by the new dolphin once he is introduced to the group.

Hypothesis: The new dolphin will exhibit more social behavior after being introduced to the group.

Question 6: Does the behavioral repertoire of the group change after the new dolphin is introduced?

Again, dolphins are highly social animals and also tend to be curious (Connor, 2007; Goold & Fish, 1998; Gregg, 2013). The introduction of a new individual should cause the group members to engage in more social activity within the group and with the new dolphin.

Hypothesis: After the introduction, there will be an increase in the amount of social activity observed.

Question 7: Is there a relationship between signature whistle production and a particular type of behavior after the new dolphin is introduced to the existing group?

Signature whistle calls are social in nature. They act primarily as cohesion calls to reunite group members (Janik & Slater, 1998) and these calls are often accompanied by social behavior (Cook et al., 2004). In the wild, signature whistles are produced during most introductions before groups intermix socially (Quick & Janik, 2012). Therefore, similar trends are expected during this study.

Hypothesis: There will be a positive relationship between signature whistle production and social behavior.

CHAPTER II - METHODS

Subjects

Data for this study was collected at the Institute for Marine Mammal Studies (IMMS) in Gulfport, MS with three Atlantic bottlenose dolphins from September, 2012 to March, 2013. The existing dolphin group consisted of Bo, an adult female, and, Buster, an adult male. Bo and Buster had been housed as a group at IMMS for 1.5 years. Before arriving at IMMS, they had been housed together at another facility.

At the time of this study, Bo and Buster were housed together in a large main pool, which was approximately 38 x 18 x 3.5 m (125 x 60 x 12 ft.) (Figure 1) with four center pens that could be closed off from the rest of pool through a system of gates. The barriers that subdivided the center pens were made from a mesh netting material, which allowed animals to see and hear one another from all areas within the pool.
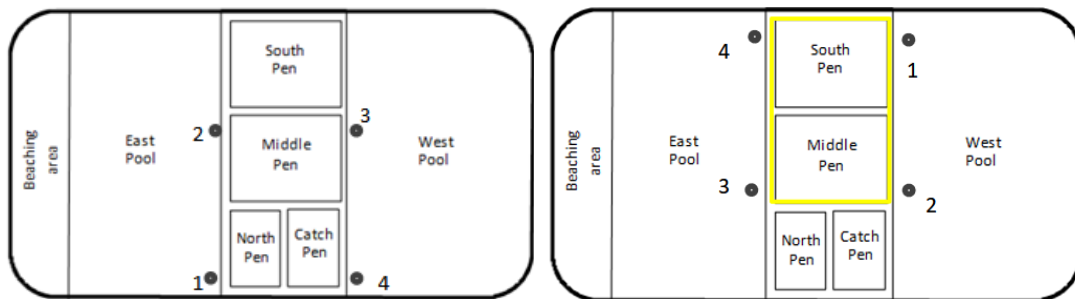
Figure 1. Main pool

Main pool with a four hydrophone array during baseline phase (left) and introduction phases (right). The central portion of the pool was sectioned off into four pens separated with mesh netting below the water and a series of walkways above. Underwater gates could be opened and closed to confine dolphins to specific areas. During the introduction phases, the new individual was sectioned off from the others in the highlighted area (right).

A stranded male dolphin, Chance, was rescued in 2011 and held in quarantine while being rehabilitated at IMMS. This dolphin was estimated to be around two to three years of age at the time of rescue and four to five years of age at the time of introduction. In the baseline phase, Chance was being held in a round pool (approx. 12 m diameter x 3 m deep) located approximately 6 m from the main pool. Due to the short distance separating the pools, it was possible that all of the dolphins could hear breaches, in-air vocalizations, interactions with trainers, and other disturbances beyond their pool. Therefore, it was possible that prior to the introduction, these individuals could have been aware of each other's presence to some degree.

Equipment

Up to four HTI-96 Min series hydrophones (frequency response: 2 Hz–30 kHz, sensitivity: -170 dB re lV/uPa) and a ZOOM R-16 8 channel digital audio recorder (sampling rate 44.1 kHz per channel, 24-bit resolution) were used to capture in-water dolphin vocalizations for Bo and Buster, housed together in the main pool, and Chance, who was moved from the round pool to the main pool during the course of this study. A four hydrophone array (Fig 1) with hydrophones placed one meter below the water's surface was used to capture underwater vocalizations of Bo and Buster during the baseline phase and all three dolphins during the other phases. Audio from each hydrophone was recorded onto a separate channel. Only one hydrophone was used to capture underwater vocalizations for the isolated dolphin during the baseline phase because localization of the sound source was not necessary.

Study Design

Primary data collection occurred during the baseline and post-introduction phases but additional data was collected opportunistically on the day of introduction and during a follow-up period after primary data collection had concluded. The baseline phase occurred from September 14 -23, 2012, approximately five weeks before the introduction on October 31, 2012. The post-introduction phase occurred November 1 - 9 and November 14, 2012. Recording for each phase took place over a ten-day period with two, semi-randomized, 15-minute recording sessions each day (Table 1). The configuration of recording sessions in each phase fell in designated time slots between the hours of 7 AM and 6 PM. Acoustic and behavioral data were also collected on October 31, 2012, which was the day of the introduction and during several follow-up sessions that occurred in December 2012, January 2013, and March 2013 (Table 2).

Table 1

Data collection schedule for baseline and introduction phases.

Date	Day	7:00 - 7:30 AM	9:30 - 10:00 AM	11:30 - 12:00 PM	1:30 - 2:00 PM	3:30 - 4:00 PM	5:30 - 6:00 PM
Baseline Phase							
9/14	1	x			x		
9/15	2			x	x		
9/16	3					x	x
9/17	4		x				x
9/18	5	x		x			
9/19	6		x			x	
9/20	7	x				x	
9/21	8				x		x
9/22	9		x		x		
9/23	10	x		x			
10/31		Day of Introduction					
Post-introduction Phase							
11/1	1	x			x		
11/2	2				x		x
11/3	3		x			x	
11/4	4			x	x		
11/5	5		x			x	
11/6	6	x					x
11/7	7					x	x
11/8	8		x	x			
11/9	9	x		x			
11/14	10			x	x		

Table 2

Dates of data collected during follow-up sessions.

Date	Hours of Audio	Behavioral Sessions
12/7/12	2.77	2
1/10/13	2.03	2
1/21/13	0.28	0
1/28/13	0.63	1
3/22/13	2.75	1
Total	8.5 hrs	6

Day of Introduction

On October 31, 2012, Chance was moved from the round pool to the main pool. Over the course of the introduction, 7.05 hours of audio from the hydrophone array in the main pool were collected. In addition, seven 15-minute behavioral data collection sessions were recorded. The introduction began with Chance being removed from the round pool for a medical examination. During this time, in-air audio and video recordings were collected over the 44 minutes of the transfer process. Audio recording in the main pool began 44 minutes before the introduction and continued with few interruptions for six hours and 20 minutes after Chance was introduced. When placed into the main pool, Chance was confined to the middle section of the pool and had access to the Middle, and South pens. He did not have access to other parts of the pool and the other dolphins were limited to the East side of the main pool. All dolphins were able to see and hear one another through the mesh barrier.

Physical Introductions

While the dolphins occupied these neighboring pools, Bo and Buster were allowed access to Chance by opening the gates between the pools at various times over several sessions. These introductions took place on three separate occasions during the

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post-introduction phase. Bo was allowed into the south and middle pool areas with Chance on two different days and Buster was allowed in once.

<center>Behavioral Observations and Recording Sessions</center>

Behavioral data collection sessions were 15 minutes in length and consisted of behavioral observations that occurred at the same time as the audio recordings. Behavioral observations were broken down into 15, one-minute intervals and were collected pool-side by trained observers. For each one-minute interval of behavioral observation, the following variables were recorded for each dolphin: date and time, coder, minute, behavioral states - dolphin's location, swim type, swim speed, and behavioral event categories (Table 3). The behavioral state of each dolphin was recorded once per minute at the beginning of the minute and all other behaviors were recorded as present or absent for each one-minute interval. Reliability for this system of coding was previously established (Lyn et al., submitted). Based on the results of the reliability analysis, it was concluded that the behavioral states and four overall event-based behavioral categories achieved reliability (85% inter-observer agreement), thus behavioral analysis was limited to these categories: behavioral state, object play, social behavior, and aggression (Table 3). The regurgitation category also achieved reliability but no regurgitation events were recorded during this study.

Table 3

Description of behaviors.

Behavioral States	Description
Stationary	Dolphin is non-mobile, resting in one position at or near the surface. Includes drifting into stationary position. For example, if moving from a circle swim to stationary, the dolphin drifts in the same direction it had been going.
Circle	Dolphin is swimming in a stereotypic pattern repeatedly. This could be any pattern, but is most often a circuit of the pool.
Non-circle	Dolphin is swimming but in an unpredictable pattern that is not repeated.
Pair swim	Two dolphins are swimming and surfacing in sync near one another
Slow	Typical swim speed
Fast	Swimming in a faster than normal speed for more than 5 seconds
Behavioral Events	**Description**
Social Behavior	One dolphin is in physical contact with the other with no evidence of aggression (no biting, raking or charging). This also includes any instance in which a dolphin focuses its attention towards another dolphin or person including looking at, touching, or acting in response to another individual.
Object Play	A dolphin is in physical contact with an object for more than 1 second.
Regurgitation	Expelling previously ingested food
Aggression/ displacement	One dolphin bites, rakes, or charges another. One dolphin attempts to enter a pool area and is blocked by the other.

Acoustic Analysis

A total of 5 hours of audio were recorded during the baseline phase, 7 hours of

audio were recorded on the day of the introduction, and 9.5 hours of audio were collected

during the post-introduction phase (Table 4). An additional 8.5 hours of audio were

recorded during follow-up sessions in the months following the introduction. Behavioral

and acoustic comparisons that were made between different phases were standardized to

account for differences in the hours of recording that took place during each phase.

Table 4

Hours of audio and number of days during each phase of data collection.

Phase	Days	Hours of Audio
Baseline	10	5
Day of Introduction	1	7.05
Post-Introduction	10	9.5
Follow-Up	5	8.50
Total	24	24.55

All acoustic data was analyzed using Raven Pro 1.5 sound analysis software

(Cornell Lab of Ornithology, Ithaca, NY) with a human observer visually examining the

frequency spectrograms (512 point FFT, Hanning window, 50% overlap). All frequency

modulated, narrow band, tonal signals were labeled as whistles by one observer, the

author (M.B.). All data was viewed twice to ensure all whistles were selected. Signals

that consisted of repeated whistles or multiple parts were considered one multi-loop

whistle when the inter-loop interval (Esch, Sayigh, & Wells, 2009), that is, the time

between the end of one whistle and the beginning of the next, was less than 0.5 seconds

(Janik & Slater, 1998).

Because data was collected using a hydrophone array, some whistles, were not

represented fully on each of the four hydrophone channels. This could occur if the sound

source was moving. For example, if a dolphin was swimming from one pool location to

another. As a result, there were some cases where the initial part of a whistle appeared on

one channel and the rest of the same whistle appeared on another channel (Figure 2). In

these cases, the whistle was assessed by the observer recreating the complete signal by

mentally combining the parts of a signal as it appeared across multiple channels.
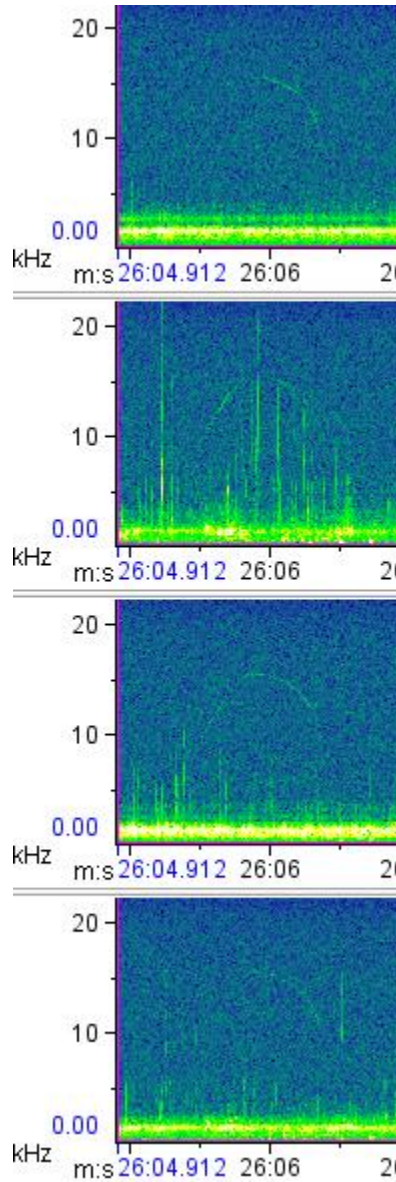
Figure 2. A single, simultaneous whistle event recorded on four hydrophone channels.

Passive Acoustic Localization

The passive acoustic localization program known as TOADy was used to identify

signature whistle matching events and vocalizations made by the group, Bo and Buster,

versus vocalizations produced by the new individual, Chance. TOADy is a Matlab program, written by Luke Rendell and has been shown to accurately localize dolphin whistles (Quick et al., 2008). This method uses the timing of audio signals from multiple audio recordings to estimate the position of the sound source (Janik et al., 2000).

Localization calibration was conducted by producing a series of test sounds at different areas of the pool. Tests sounds were created by clicking a pair of dive weights together. Calibration results and sources of error are discussed in Appendix A. Only 10 of the 36 calibration points could be localized. In addition, biases revealed during the error assessment showed a high rate of false positive localizations to the inner array areas. Because of this bias, localizations of whistles that indicated the sound source originated from inside the array were not considered accurate.

<div align="center">Signature Whistle Determination</div>

The operational definition of a signature whistle is the predominant whistle contour produced while a dolphin is in isolation (Caldwell et al., 1990; Janik & Slater, 1998; Sayigh et al., 1990). In cases where recordings in isolation are not obtainable, there are several other methods that can be used to confirm an individual's signature whistle. For this study, a combination of methods were used and each method is described in detail in the following sections. Signature whistle determination methods included a simple classification method, classification by naïve raters, and bout analysis. Localization was also used to provide additional evidence to identify Bo's whistle. Several other classification methods exist but classification of whistles into distinct categories by human raters has been shown to be more reliable than computer

classification and is commonly used in acoustic research (Janik, 1999; Sayigh et al., 2007).

Simple Classification Method

This signature whistle classification method involved examining vocalizations produced when a dolphin was in complete isolation, either in a pool, out-of-water during transport, or pool-side during a medical examination. The spectrogram images of each whistle were sorted into contour categories by one experienced rater, M.B. who was aware that only one dolphin was producing all of the whistles present in the recording. After all whistles had been placed into groups, the percentage of whistles contained in each category was calculated. The category containing the most whistles was deemed the signature whistle if it contained a clear majority (>10% more whistles) compared to the other categories.

Classification by Naïve Raters

The classification by naïve raters method was similar to the simple classification method, except multiple raters that were blind to condition and whistle owner, independently matched whistles to an exemplar signature whistle type from a catalog of whistles (Appendix C) and rated the similarity of the whistles on a scale of 1 to 5, with 5 being highly similar and 1 being highly dissimilar. Five naïve raters completed training and then rated a random subset of 20% of the whistles chosen from the full dataset. Inter-rater reliability of the template choices and scores of the raters as well as M.B. was conducted to confirm that the M.B.'s ratings for the entire dataset were accurate and could be used for analysis of the full dataset (see Appendix B for procedure and results).

Bout Analysis

Signature whistles are often produced in bouts that occur within 1-10 seconds of one another (Janik et al., 2013). Analysis of whistle bouts, also known as the signature identification (SIGID) method can be used to identify the signature whistles of free-swimming, wild dolphins (Janik et al., 2013; King & Janik, 2013; Kriesell, Elwen, Nastasi, & Gridley, 2014; Luís et al., 2015; Quick & Janik, 2012). An analysis of bouts was used to determine if the dolphins in this study were producing signature whistles in a way that was similar to other dolphins and to identify Bo's signature whistle. A bout was defined as a sequence of three or more whistles with an inter-whistle interval of 10 seconds or less. Probable and possible matches, as well as non-target whistles were excluded when calculating inter-whistle intervals.

Localization

Passive acoustic localization was used to confirm Bo's signature whistle and identify whistle copying or matching events. Over the course of this study, Bo and Buster self-isolated on several occasions. Whistles produced while the dolphins were isolated were localized to determine the area of the pool in which the whistles originated. The localization results were then compared to the behavioral data, which indicated which area of the pool each dolphin was occupying at the time the whistles were produced. Identification of signature whistle copying was attempted using the same method. Signature whistles that originated from an area of the pool where the owner of that whistle was not present, but another dolphin was present, were deemed signature whistle copies.

Signature Whistle Determination

Buster's signature whistle was determined using the simple classification method and data that was previously collected while Buster was held out-of-water during transport. Chance's signature whistle was determined using the simple classification method to categorize whistles that were recorded during the baseline phase of the study. Bo's signature whistle was determined through a combination of simple categorization, bout analysis, and passive acoustic localization.

Analytical Methods

Chi-square tests of independence and goodness of fit tests were used to answer questions involving whistle counts and frequencies of behaviors. Chi-square calculations were done using Microsoft Excel™ or an interactive online calculator for chi-square (Preacher, 2001). A penalized likelihood logistic regression, also known as a Firth logistic regression, was used to describe the role of behavior, phase, and individual differences in signature whistle production. The Firth regression is optimal when dealing with rare event data (Firth, 1993), in this case, the occurrence of intervals where signature whistles were detected. The test was performed in SPSS 24 using the Essentials for R Plugin and R version 3.2.2. All other statistical tests were conducted using SPSS 24.

CHAPTER III - RESULTS

In all, there were 26 days of data collection. Behavioral data collection resulted in 53 behavioral observation sessions totaling 13.25 hours. Audio recording resulted in a total of 25.55 hours of audio that contained 5,358 whistles. The total number of whistles recorded during each phase is presented in Table 5. There was an unequal number of recording hours across phases so, for statistical analysis, whistle counts were standardized in order to compare the number of whistles produced per hour. Fewer behavioral observations were available for the day of introduction and follow-up phases so direct behavioral comparisons were limited to comparisons of the baseline and post-introduction phases.

Table 5

Total number of observations sessions, observation hours, recording hours and whistles recorded in each study phase.

	Collection Days	Observation Sessions	Observation Hours	Recording Hours	Whistles
Baseline	10	20	5	5	1106
Day of Introduction	1	7	1.75	7.05	345
Post-Introduction	10	20	5	9.50	1946
Follow-up	5	6	1.50	8.50	1961
Total	26	53	13.25	25.55	5358

Signature Whistle Determination

Buster

In-air recordings taken when Bo and Buster were transported to IMMS in 2011 were used to identify Buster's signature whistle. Recordings captured 49 whistles produced by Buster, 69% of which were classified as the same whistle type and thus were deemed to be his signature whistle (Figure 3). It is highly probable that Buster had an

even higher proportion of signature whistles in both the out-of-water dataset as well as the full dataset for the entire study. Many of the whistles that were not considered a match were likely partial signature whistles that did not contain enough features to be considered a match. The distinguishing features of Buster's signature whistle were not always captured by the hydrophones. For example, Figure 4 shows a single, simultaneous whistle event recorded on the day of introduction. This whistle was visible on two different hydrophone channels. Both images show Buster's signature whistle but the top image shows the full whistle while the bottom image shows that the hydrophone did not capture the full signal. The bottom image matches both Buster's whistle and another variant whistle type that was observed in the dataset.
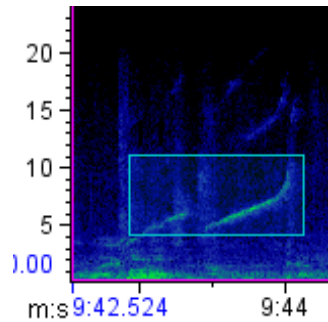
Figure 3. Buster's Signature Whistle
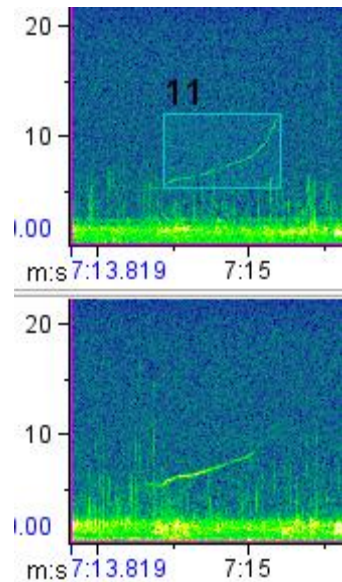
Figure 4. Spectrogram image of a single, simultaneous whistle event visible on two hydrophone channels.

Chance

Because Chance, the new individual, was isolated during the baseline phase, the hydrophone recordings from this period were used to determine the most common whistle type produced. Whistles produced by Chance during isolation were categorized into common types by M.B. According to M.B.'s classification of all whistles, the predominant whistle type used by Chance during isolation made up 85% of 1,019 whistles that were produced during this time and this was deemed to be his signature whistle (Figure 5). Naïve human raters supported this conclusion when they rated a subset (20%) of the full dataset. Based on the ratings, 86% of the subset of whistles recorded while Chance was in isolation were similar (average rating ≥3) to the predominate whistle type as classified by M.B.
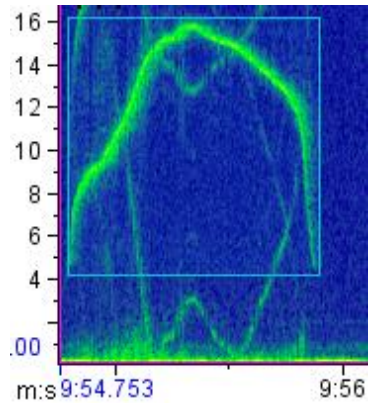
Figure 5. Chance's signature whistle.

Bo

Bo was transported to IMMS with Buster in 2011, but during this time no whistles from Bo were captured by any of the recording devices. Therefore, three different methods were used to determine Bo's signature whistle using the recordings collected during this study (Figure 6).
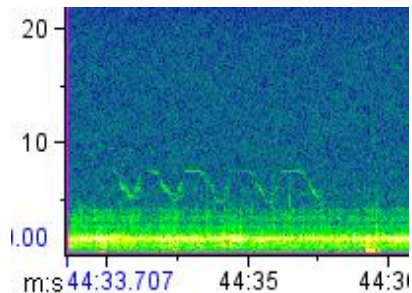
Figure 6. Bo's signature whistle.

The first method involved simple classification with one observer, M.B., classifying all whistles from the entire dataset into similar types (see Appendix B Table A2 for classification criteria). A subset of whistles collected during self-isolation events was also analyzed. In order to be included in the analysis, the dolphin needed to be in isolation one minute prior to the whistle until one minute after the time in which the whistle occurred. During the baseline phase, Bo and Buster self-isolated to different pool

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areas for a total of 14 minutes over five different sessions. During the post-introduction

phase, they were separated from each other for a total of 83 minutes over eight different

sessions. During this time, three different whistle types were commonly produced, two of

these were the signature whistles of the other two dolphins, Buster and Chance. The third

most common whistle type was a sine wave whistle (Figure 6) with a frequency range of

4 - 8 kHz, suspected to be Bo's signature whistle. This whistle appeared five times more

often than all of the other major non-signature whistle types combined (Table 6). This

difference was not only statistically significant (binomial test, $p < .01$) but was also

notable in that this is a subcategory type that dominated all other major categories, each

of which contained multiple subcategories. Within the full dataset, this particular sine

wave whistle was still highly stereotypical and was one of the most common whistle

types observed.

Table 6

Whistle types in dataset.

Type	All Whistles	Self-Isolation
Chance	3560	163
Chance Probable	590	74
Bo	225	49
Bo Probable	9	2
Buster	128	11
Buster Possible	430	56
Positive Slope	183	9
Negative Slope	10	1
Sine Wave	94	7
Flat	116	9
Indeterminate	14	2

The number of whistles of each type produced overall and when Bo and Buster self-isolated. Probable and possible whistles are those

that could not be confirmed as a match because they were only partial whistles, however, the partial contour shape and frequencies

matched the exemplar perfectly. Probable and possible whistles were not included in signature whistle analyses.

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The second method used to determine Bo's signature whistle was the localization of the suspected sine-wave signature whistle during self-isolation time periods. Seven of the 11 sine wave whistles could be localized and all seven whistles were confirmed to have originated from the area of the pool where only Bo was present (Table 7). One other whistle could also be localized to an area of the pool where Bo was present, but the caller could not be determined because both Bo and Chance were occupying the area where the sound originated. Localization was not possible for the remaining whistles. Although all whistles that could be localized indicated that Bo was the likely caller, five of the seven localizations indicated that the call could have originated from inside of the array which included the Middle and South pool areas. Because of the bias toward inner-array areas and the 0-7 m potential error that was displayed during the calibration, confirmation that the sine wave whistle was Bo's signature whistle required further evidence.

Table 7

Localization results for Bo's whistle.

	Phase	Localized Area	Bo's Location	Buster's Location	Chance's Location
1	Baseline	Middle	Middle*	West	Not Present
2	Post Introduction	West	West*	East	Middle
3	Post Introduction	South/West	West*	East	Middle
4	Post Introduction	West	West*	East	Middle
5	Post Introduction	Middle/South	South*	East	Middle*
6	Post Introduction	West	West*	Middle	Middle
7	Post Introduction	South/West	West*	Middle	Middle
8	Post Introduction	South/West	West*	Middle	Middle

Localization results and dolphin locations for eight sine wave whistles thought to be Bo's signature whistle. Asterisks indicate the areas where the dolphin's location coincide with the localization results.

The third method used to determine Bo's signature whistle was a bout analysis. The bout analysis was performed to determine if the sine wave whistle in question was

being produced in a manner consistent with how signature whistles are typically produced. This sine wave whistle type, suspected to be Bo's signature whistle, was produced in bouts a total of 10 times over the course of the study with bouts ranging from three to six whistles per bout. The average bout consisted of four whistles. The production of bouts in this manner is consistent with how signature whistles are typically produced (Janik et al., 2013). Based on the evidence provided by the localization results, the number of times this whistle was recorded, and the bout analysis, this sine wave whistle was labeled as Bo's signature whistle.

Behavioral Description of Initial Introduction

Detailed behavioral observations took place during the initial introduction and in a follow up session 1.5 hours following the initial introduction. Observation began at 10:23 A.M (CDT). and Chance was added to the middle pool section three minutes later. Immediately after introduction, Chance began circle swimming almost continuously for the rest of the observation session (11 of 13 one minute intervals). Buster, who had been circle swimming in the two intervals prior to the introduction, began non-circle swimming, spy hopping, and leaped once during interval 3 when Chance was added, before continuing to swim in circles for the remainder of the observation session. He was also seen spy hopping during two additional intervals. Bo, who had been non-circle swimming in the two intervals prior to the introduction, continued this swim behavior until interval 5 then began switching between circle swimming and remaining stationary at one location (five intervals stationary, five intervals circle swimming). Bo was seen spy hopping during interval 2, before Chance was added and continued occasional spy hopping for the remainder of the session (9 of 13 intervals). It was unclear if she was spy

hopping to view Chance or to view the trainers who had just added Chance to the pool. After the introduction, she was also seen swimming and remaining stationary near the gate looking into the middle pool area where Chance was located (4 of 13 intervals).

Behavioral observation was repeated approximately 1.5 hours following the initial introduction when no trainers were present. Chance and Bo were non-circle swimming for almost the entire session (Chance 14 of 15 intervals, Bo 12 of 15 intervals). For the remaining intervals, Chance lapsed into circle swimming while Bo was stationary. Occasionally, Bo also appeared to be spy hopping in order to view Chance (4 of 15 intervals) and remained near the gate to the middle pool area where Chance was located (5 of 15 intervals). Buster continued circle swimming during the entire session (15 of 15 intervals) and did not engage in any other behaviors. Combined whistle rates per hour decreased on the day of introduction and then returned to baseline levels during the post-introduction and follow-up periods (X^2 (df=3, $N = 706$) = 124.754, $p < .001$, Cohens's w = .42) (Figure 7). Signature whistle production followed a similar pattern making up 36% to 79% of combined signature whistle production per hour during each phase and these differences were also significant (X^2 (df=3, $N = 519$) = 133.37, $p < .001$, Cohen's $w =$ .51).
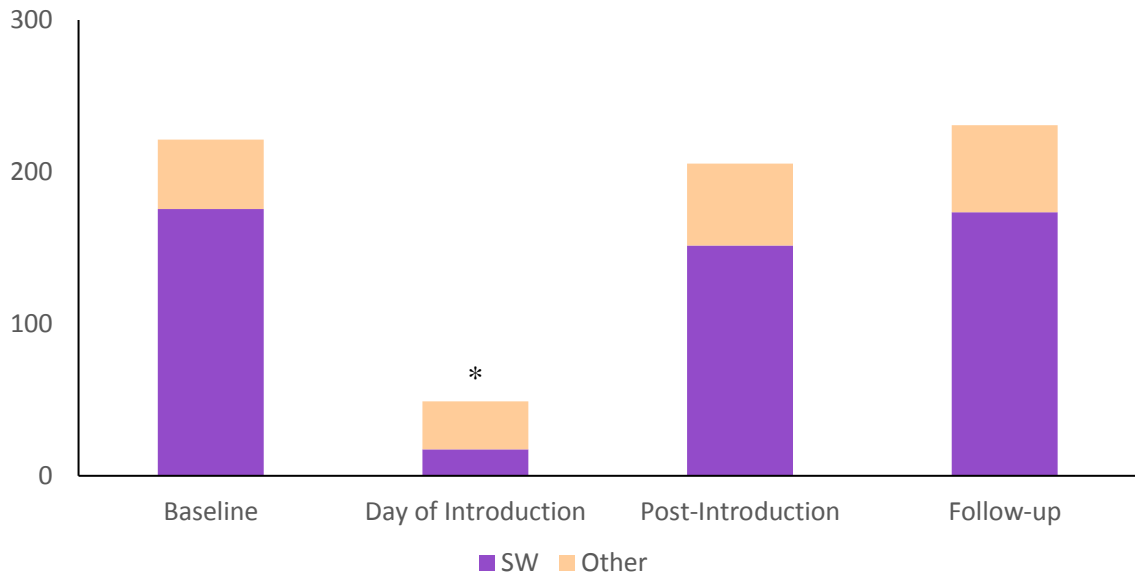
Figure 7. Combined whistle production per hour during each phase of the study.

Signature whistle rates and rates of other whistle types are represented by different colors. Asterisks indicates significant differences ($p < .05$).

Signature whistles for each dolphin were produced at significantly different rates across different phases of the study (X^2 (df=6, $N = 518$) = 182.595, $p < .001$, Creamer's V = .20) (Figure 8). The new individual's whistle (Chance's whistle) was observed significantly more often than all other whistle types combined during the baseline, post-introduction, and follow-up phases, (binomial test, $p < .001$). Chance's whistle, along with Buster's, was the least common whistle produced on the day of introduction (X^2 (df=3, $N = 49$) = 41.69, $p < .001$, Cohen's $w = .9$).
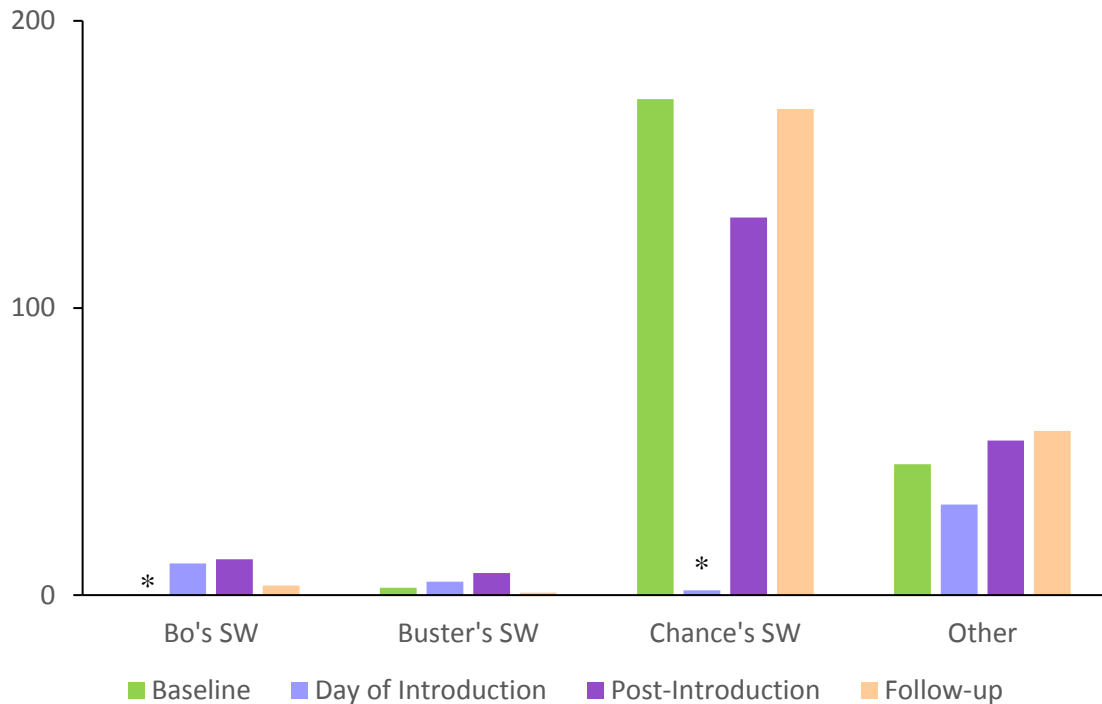
Figure 8. Whistle rates per hour

Rates during each phase of the study for each dolphins' signature whistle (SW) and other whistles that were produced. Asterisks indicates significant differences ($p < .05$).

The rate of whistle production for Bo's signature whistle significantly increased on the day of introduction $(X^2$ (df=3, $N = 26) = 16.15$, $p = .001$, Cohen's $w = .79$), while rates for Chance's whistle fell significantly $(X^2$ (df=3, $N = 475) = 162.095$, $p < .001$, Cohen's $w = .58$) (Table 8). Buster's overall signature whistle rate was lower than that of both Chance and Bo (binomial test, $p < .001$, $p = .03$, respectively) and was too low to conduct statistical analysis comparing across phases. Whistle rates for whistles that were not classified as signature whistles ("Other") were higher than the rates of Bo and Buster's whistle types in all phases (baseline: X^2 (df=2, $N = 49) = 81.1$, $p < .001$, Cohen's $w = 1.29$; day of introduction: X^2 (df=2, $N = 48) = 25.125$, $p < .001$, Cohen's $w = .72$; post-introduction: X^2 (df=2, $N = 74) = 52.65$, $p < .001$, Cohen's $w = .74$; follow-up: X^2

(df=2, $N = 61$) = 99.28, $p < .001$, Cohen's $w = 1.28$). Chance's whistle was produced

more often than non-signature whistles in all phases except for on the day of introduction

(X^2 (df=1, $N = 34$) = 26.47, $p < .001$, Cohen's $w = .43$).

Table 8

Signature whistle rates per hour.

	Bo's SW	Buster's SW	Chance's SW	Other Whistles
Baseline	0	3	173	46
Day of Introduction	11	5	2	31
Post-Introduction	12	8	131	54
Follow-up	3	1	169	57
Total	27	16	475	188

Whistle rates per hour for each dolphin's signature whistle (SW) and all other whistles during each phase of the study.

Table 9 contains the standardized number of bouts produced in a five-hour period.

Chance's whistle appeared in far more bouts than the whistles of the other dolphins and

Buster's whistle appeared in fewer bouts, with fewer whistles per bout, than either of the

other dolphins (X^2 (df=2, $N = 118$) = 190.49, $p < .001$, Cohen's $w = 1.27$). The pattern of

bout production was similar to the rates of signature whistle production seen over the

course of the study, with a sharp decline in bout production seen for Chance's whistle on

the day of introduction and a sudden and consistent increase in bout production for Bo's

whistle on the same day.

Table 9

Bout production.

	Phase					# of Whistles in Bout	
	Baseline	Day of Introduction	Post-Introduction	Follow-Up	Total	Average	Range
Chance	21	1	40	48	110	37	3-232
Bo	0	3	1	1	5	4	3-6
Buster	0	1	1	1	3	3	3

Standardized number of bouts produced per five hours in each phase and overall as well as the average number of whistles present in a bout and the range of minimum and maximum whistles present in bouts for each dolphin's whistle.

The production of whistle loops was also analyzed. Bo's signature whistle was a connected multi-loop whistle that was often produced with a varying number of loops. The majority of the time, Buster's signature whistle was presented as a single loop element; however, at times the whistle was seen with multiple disconnected loops. Chance's signature whistle typically consisted of one loop. Table 10 shows the whistle counts per hour for multi-loop whistles. Both Buster and Chance produced more multi-loop whistles per hour during the follow-up phase, although counts were too low to perform statistical analysis. Bo's whistle was a connected multi-loop whistle, thus the counts per hour for her whistle closely resembled the total signature whistle counts for her whistle.

Table 10

Multi-loop whistle production.

Phase	Bo	Buster	Chance
Baseline	0.20	0.20	16.80
Day of Introduction	12.06	0.14	0.00
Post-Introduction	12.25	1.16	4.33
Follow-Up	2.71	0.24	8.12

Number of multi-loop whistles per hour for Bo, Buster, and Chance during each phase of the study.

The average number of loops and ranges for multi-loop whistles are presented in

Table 11. Bo's whistle contained an average of three loop elements with a range of 1.5 to

seven loops, Buster's whistle, when presented as a multi-loop whistle, typically consisted

of two loop elements but ranged from two to four elements, and Chance's whistle, when

presented as a multi-loop whistle, contained between two and six loop elements.

Statistical analysis comparing the average number of loop elements across phases was not

possible, but the average and range of loop elements was largely consistent across phases

except for on the day of introduction when Chance did not produce multi-loop whistles

(Table 11).

Table 11

Average number of loop elements.

Phase	Bo	Buster	Chance
Baseline	2.5	4	2.3 (2-6)
Day of Introduction	3 (1.5-7)	2	0
Post-Introduction	3.2 (1.5-6.5)	2.3 (2-4)	2.1 (2-3)
Follow-Up	2.8 (1.5-4.5)	2.5 (2-3)	2.4 (2-6)

Average number of loop elements for each dolphin during each phase of the study with the range listed in parentheses. No range is

listed when only one multi-loop whistle was present.

Bo and Buster were physically introduced to Chance separately on several

occasions during the post-introduction phase. The results of a 2-way factorial ANOVA

showed that there was no change in the signature whistle production rate of each dolphin

when Bo or Buster were allowed to swim in the middle section with Chance (F (1,39)

= .001, p = .978, partial η^2 = 0).

In addition to the localization results reported above, seven additional whistles

were localized to an area of the pool occupied by only one dolphin (Table 12). Due to the

quality of the data, localization was not possible for the vast majority of whistles and

localization results that indicated a whistle originated from inside the array could not be included in the analysis. Signature whistles were localized on two occasions, both belonging to Buster. Once, Buster's whistle was localized to an area of the pool occupied by Buster and the other time it was localized to an area of the pool occupied by Bo. All other whistles were either partial or variant non-signature whistles. Because of this, there was only one instance where possible whistle copying was observed, when Bo produced Buster's whistle.

Table 12

Additional localization results.

Phase	Localized Area	Dolphin Present	Whistle
Post Introduction	East	Buster	Non-SW
Post Introduction	South*	Bo	Non-SW
Post Introduction	East	Bo	Non-SW
Post Introduction	West	Bo	Buster's SW
Post Introduction	East	Buster	Buster's SW
Follow-Up	Middle*	Chance	Non-SW
Follow-Up	Middle*	Chance	Non-SW

Localization results for seven additional events where dolphins self-isolated to different pool areas. Asterisks indicate localization results for inner-array areas.

During the matching event, Buster's signature whistle was localized to the west pool where Bo was the only dolphin present. Buster was located in the east pool and Chance was located in the middle pool during the entire 15-minute observation session in which the event occurred. Although this whistle was preceded by two other whistles of the same type, all within 2.5 seconds of one another, those whistles could not be localized; therefore, it is unknown if Bo was producing Buster's signature whistle in a bout, or if Bo was producing Buster's whistle in response to Buster producing his signature whistle.

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The swim behaviors of Bo, Buster, and Chance (the new individual) were compared in separate analyses for baseline and post-introduction phases to determine if the behavioral repertoire of the new dolphin or the group changed after introduction. Pair swimming was excluded from this test because it was not possible for Chance to engage in this behavior, as he was physically isolated from the group during both phases. During the baseline phase, there was a significant difference among the swim patterns of the dolphins (X^2 (df=4, $N = 884$) = 317.078, $p < .001$, Creamer's $V = .299$) (Figure 9). Circle swimming comprised a large majority of Buster's swim behavior with very little stationary behavior and almost no non-circle swimming, Bo primarily engaged in stationary behavior followed by circle swimming, and Chance was observed non-circle swimming and circle swimming almost equally with only 9% of his time spent in stationary behavior.
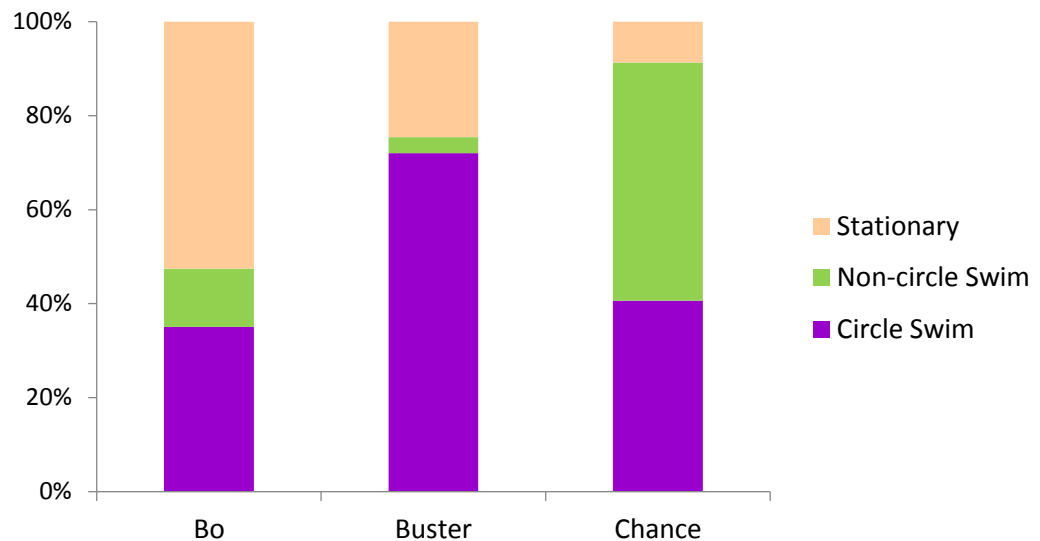
Figure 9. Swim behavior of Chance, Bo, and Buster during the baseline phase.

There were also significant differences in swim behavior among dolphins during the post-introduction phase, although these differences were less pronounced than during

baseline (X^2 (df=4, $N = 894$) $= 223.42$, $p < .001$, Creamer's $V = .25$) (Figure 10). Both Bo

and Buster's swim patterns were similar to their baseline behavior. Chance's swim pattern

changed more dramatically with a two-fold increase in circle swimming, a four-fold

decrease in non-circle swimming, and a 13-fold decrease in stationary behavior (X^2

(df=2, $N = 600$) $= 141$, $p < .001$, Creamer's $V = .34$).
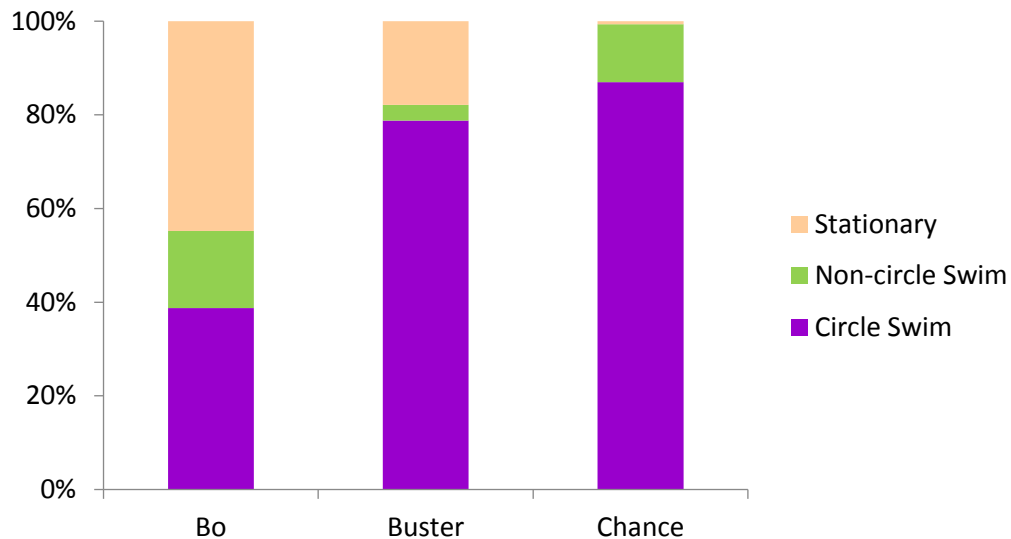
Figure 10. Swim of Chance, Bo, and Buster during the post-introduction phase.

Although there were individual differences in each dolphin's swim patterns, Bo

and Buster maintained their own swim patterns between baseline and post-introduction

phases. Even with pair swim behavior included, no significant differences were found

between the individual swim patterns of these two dolphins between phases (Bo X^2

(df=3, $N = 600$) $= 7.166$, $p = .07$, Creamer's $V = .06$; Buster X^2 (df=3, $N = 600$) $= 5.677$,

$p = 1.28$, Creamer's $V = .06$). Pair swimming was much less common than the other

swim behaviors, but it was notable that three times as much pair swimming was observed

during the baseline phase than in the post-introduction phase. Pair swimming between Bo

and Buster occurred 9 times during the baseline phase and 3 times during the post

introduction phase. Statistical analysis of pair swimming was not possible due to the low number of observed frequencies.

There were no observable differences in social behavior between the baseline and post-introduction phases for any of the dolphins. Both Bo and Buster were observed engaging in social activity twice during each phase. Chance was never observed engaging in social activity, even though during the post-introduction phase it was possible for him to interact with the other dolphins along the mesh barrier that separated the pools. Statistical analysis of social behavior was not possible due to low observed frequencies.

There were differences in object play behavior for Chance, as well as the group members during baseline and post-introduction phases. Chance played with objects significantly more during the baseline phase (X^2 (df=1, $N = 116$) = 98.7, $p < .001$, Cohen's $w = 0.93$); object play was observed 112 times during baseline and only four times during the post-introduction phase. The opposite was true for Bo and Buster. Although statistical analysis was not possible due to low observed frequencies, both Bo and Buster were each seen interacting with objects only once during the baseline phase and 8 times during the post-introduction phase.

The primary behaviors of interest, social behavior and object play, could not be compared because they occurred too infrequently. However, for the entire dataset, the swim behavior and co-occurrence of signature whistles for each dolphin was compared using a chi-square test of independence in order to determine if there was a relationship between the production of signature whistles and a particular type of behavior. For each dolphin, one-minute intervals where the swim behavior occurred and signature whistles were present were compared to intervals where the swim behavior occurred but signature

whistles were not present. For all three dolphins, there were more intervals of each behavioral type where signature whistles were not observed than intervals where signature whistles were observed. For Chance, there was no difference in the proportion of intervals with and without signature whistles for each swim behavior meaning that Chance seemed to produce signature whistles regardless of his swim behavior. Results for Bo were significant (X^2 (df=3, $N = 810$) = 18.85, $p < .001$, Creamer's $V = .08$) and were nearing significance for Buster (X^2 (df=3, $N = 810$) = 7.24, $p = .065$, Creamer's $V = .05$), indicating that signature whistling co-occurred with some swim behaviors more than others and these differences were not solely an artifact of preferences in swim style.

Figure 11 shows the percentage of intervals for each swim behavior where signature whistles were present. Generally, there was less signature whistling observed when dolphins were stationary and more signature whistling when they were circle swimming. Bo and Buster had similar patterns of signature whistling across swim behaviors, but Chance's patterns were different in that his signature whistle was observed almost equally when he was circle swimming and non-circle swimming.
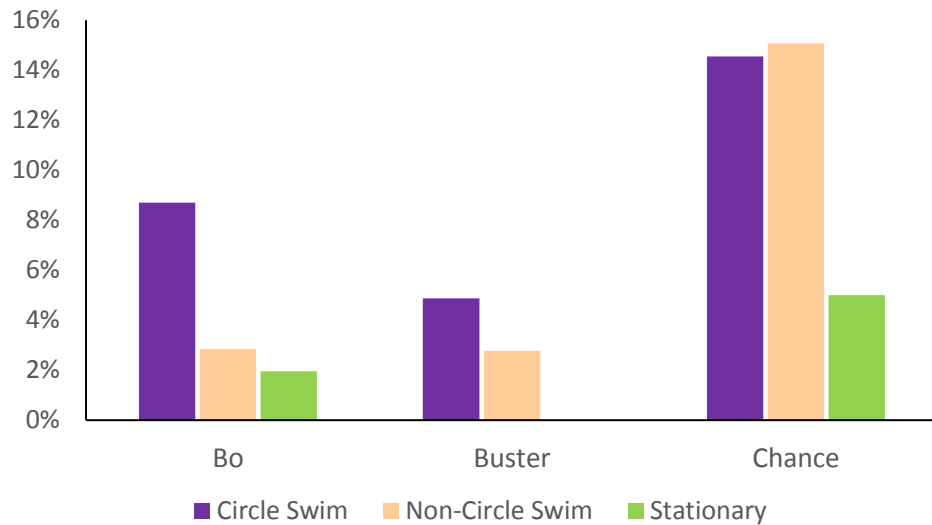
Figure 11. Swim behavior and signature whistle production.

Percentage of intervals for each swim behavior where signature whistles were present for each dolphin. There were no signature whistles observed for pair swimming for any dolphin.

The results of a Firth logistic regression showed only three specific predictors (stationary behavior, the day of introduction, and Chance) were significant and these findings were consistent with the results reported above. Signature whistling was 77% less likely to occur when dolphins were engaging in stationary behavior compared to when they were circle swimming ($X^2 = 22.77$, $p < .001$, OR = .23, (CI = -2.23 to -0.82)). The test also confirmed that signature whistling was 52% less likely to occur on the day of introduction compared to the baseline phase ($X^2 = 5.69$, $p = .017$, OR = .48, (CI = -1.44 – 10.13)) and intervals containing Chance's whistle were 3.5 times more likely than those of Buster ($X^2 = 39.85$, $p < .001$, OR = 3.5, (CI = 0.85 – 1.69)).

CHAPTER IV - DISCUSSION

There are very few publications documenting dolphin behavior during an introduction and there are none that describe the use of signature whistles in this context. The few behavioral reports that exist consist mainly of basic descriptions rather than quantitative analysis. Because of the rarity of the information provided here, both the use of signature whistles as well as behavior will be discussed in detail.

Signature Whistle Production

The ratio of signature whistles to non-signature whistles produced in each phase of the study showed that, the majority of the time, signature whistles were more common than non-signature whistles. This may have been because the new dolphin, Chance, remained physically isolated from the others, or this could be a typical response during an introduction. Dolphins are known to produce signature whistles at higher rates when they are in isolation or separated from their group (Caldwell et al., 1990; Smolker et al., 1993). They also tend to produce signature whistles when they encounter other dolphins (Quick & Janik, 2012). In this study, both situations occurred, so the high rates of signature whistle production could have been due to one or both factors.

The only phase in which signature whistles did not make up the majority of whistles produced was on the day of introduction. Unexpectedly, combined whistle production per hour dropped by 80%, then recovered during the post-introduction and follow-up period. The decline in whistle production may have been a result of individual differences in personality, reactions to stress, or due to the ages of the animals being introduced. Signature whistle production made up 78-79% of whistles produced per hour in the baseline, post-introduction, and follow-up phases indicating that, by the end of the

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study, signature whistle production had recovered. The recovery of signature whistle production to baseline levels following an introduction may be an indicator of acclimation to the environment and/or acclimation to the new social grouping. Based on signature whistle rates, it appears as though acclimation may have occurred within one month following the initial introduction; however, this pattern of whistle production should be interpreted in relation to the whistle production of each individual dolphin.

Because Chance was semi-isolated from the others after introduction, it was hypothesized that Chance, the new individual, would vocalize his own signature whistle more often than Bo and Buster upon introduction. The results show that, for the day of introduction, the opposite was true. Although Chance's signature whistle was, by far, the most common whistle type observed overall and is responsible for the combined pattern of whistle production that was observed over the course of the study, Chance's whistling declined substantially on the day of introduction. Also on this day, there was a sudden increase seen for Bo's whistle, which could indicate that Bo was attempting to communicate with Chance, the new arrival. Bo's whistle continued to appear at similar rates throughout the rest of the study, while Chance's whistle rate gradually increased and reached baseline levels at the end of the study period. During the baseline phase, Chance was in isolation and during the introduction phase he was still physically isolated from the group. This could be why Chance's signature whistle rate did not remain at lower levels.

Overall whistle rates for "other" whistles were 15 times higher, on average, than the whistle rates for Bo and Buster's whistles (Table 8), although, it is possible that many of the whistles listed as "other" were partial signature whistles of Buster and Chance (see

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Table 6 for probable and possible signature whistles estimates for each dolphin). Because

Buster's signature whistle was less distinctive than the signature whistles of Bo and

Chance, is it likely that the counts for Buster's whistle are underestimates. The

distinguishing features of Buster's whistle often carried the least amount of energy, thus,

those features were often not captured by the hydrophones. Buster's whistle also closely

resembled another commonly produced whistle type. As a result, there were many

whistles that were possible matches to Buster's whistle but they did not contain enough

features to achieve a rating high enough to be classified as a certain match. Chance's

signature whistle estimates are also underestimated because he often produced what

appeared to be partial signature whistles. Dolphins are reported to produce partial

signature whistles when they are excited (Caldwell & Caldwell, 1977). These partial

whistles were seen throughout baseline recordings where he was the only animal in the

pool. They were also seen in other phases of the study, but due to a lack of distinguishing

features, they could not be classified as his signature whistle. Bo's whistle was highly

distinctive and was dissimilar to all other signature whistle and variant types observed.

As a result, there were fewer cases where partial whistles were listed as "probable"

signature whistles for Bo's whistle type. Because of these differences, the whistle rates

reported for Bo's whistle are a more reliable indicator of actual signature whistle

production in this context.

The number of bouts reported, like the number of signature whistles reported, is

likely underestimated due to the large number of probable and possible signature whistles

that were recorded. It is also possible that some bouts may contain whistle matching

events, although this was not able to be determined due to the inability to localize the

majority of whistles produced. Therefore, it was not possible to determine if whistle matching between the new individual, Chance, and the group, Bo and Buster, did or did not occur. Whistle matching, involves two or more individuals vocalizing the same whistle within a very short timeframe of up to a few seconds. Thus, it is possible that some of the signature whistles that appeared to be produced in a bout were really two different dolphins producing the same whistle.

<div align="center">Behavioral Patterns</div>

Only one behavior was significantly linked to signature whistle production. All three dolphins produced fewer signature whistles while engaging in stationary behavior. Dolphins rest and sleep while hovering near the surface of the water, at bottom of the pool, or by swimming slowly in a fixed pattern (McCormick, 1969; Sekiguchi & Kohshima, 2003). Dolphins are also reported to produce fewer sounds when engaging in resting behaviors (Sekiguchi & Kohshima, 2003), so it is not unusual that fewer signature whistles were produced while dolphins engaged in stationary behavior. Bo produced more signature whistles when circle swimming, but differences between signature whistle production paired with circle or non-circle swimming were more evenly distributed for Buster and Chance. The reasons for these differences are unclear but they could be due to factors such as sex or individual differences.

An increase in social behavior, particularly for the new individual, Chance, was expected following the introduction, but this was not observed during the post-introduction phase. Social behavior also remained the same for both group members, Bo and Buster, during both phases. These results should not be taken to mean that Chance exhibited no social activity at all after his introduction to the group, as behavioral

observations were only conducted twice each day for a total of 30 minutes. Social interactions between Chance and the group, primarily with Bo, the adult female, were observed on several occasions by researchers and staff outside of the observation periods (personal observation). More social activity may have been observed if the dolphins had not been physically separated. However, even when Bo and Buster were allowed into the middle pool area with Chance during the post-introduction phase, social activity was still not observed. This could be the result of standard behavior due to differences in age - when a younger, subordinate dolphin is introduced to older, more dominant dolphins. Alternately, the lack of social activity could be a result of individual differences in personality (Highfill & Kuczaj II, 2007). This behavior could also be typical of dolphin introductions, as affiliative social behavior during dolphin introductions is not reported in the literature. Comparisons with additional dolphin introductions could help determine how common social behavior is during an introduction and if the occurrence of social behavior signals an important change in group dynamics.

<div align="center">Response to Stress</div>

For this study, several behavioral changes were observed that indicated that the move to a new environment was a substantial disturbance event for the new individual, Chance. When dolphins experience stress, they are known to respond by either increasing or by ceasing whistle production (Caldwell et al., 1990). On several occasions, recordings were taken of Chance while he was out of water undergoing transport or medical examinations. While out-of-water, Chance emitted very few whistles and those were not captured by the recording devices. Based on Chance's lack of vocalization when out-of-

water and on the day of introduction, ceasing vocalization appears to have been Chance's

standard response to stress.

Are multi-loop whistles indicators of stress?

The number of loop elements may or may not contain meaning or convey

additional communicative information in this situation. The number of loop elements is

reported to change based on the motivational state of the animal, with the number of loop

elements increasing with added stress; although, this measure may not be as reliable as

other measures (Esch, Sayigh, Blum, et al., 2009) For this study, Chance appeared to be

more stressed on the day of introduction when no loops were produced so this

explanation is unlikely. An alternate explanation is that the increase in loop elements

could result from an increased motivation to communicate (Esch, Sayigh, Blum, et al.,

2009). It could also be a function of whistle rate, as a faster whistle rate could result in

single, disconnected whistles that appear to be one multi-loop whistle. Both of these

explanations are plausible. Further studies are needed in order to determine how dolphins

may interpret this information and if the number of loop elements contains any

information beyond emotional state.

Behavioral indicators of stress

Swim behavior in dolphins can provide another means for assessing the stress

levels of an animal in the short and long term. Ridgway (1990) reported that newly

captured dolphins swam in circles almost continuously but, over time, circle swimming

decreased as they became accustomed to their new environment. *Stereotypy* is a term

used to describe the performance of a repetitive behavior that cannot be easily interrupted

and serves no obvious function (Mason, 1991). In dolphins, circle swimming is often

considered a stereotypical behavior (Frohoff, 2004; Sobel, Supin, & Myslobodsky, 1994). Although the focus of stereotypy in animal welfare studies has referred to it as a negative indicator (Mason, 1991), in some cases, it may be more accurate to refer to stereotypy as an indication of increased arousal, which may be normal for some animals. Several studies have indicated that species that typically have large territories in the wild frequently engage in certain stereotypical travel patterns while in a captive setting (Clubb & Mason, 2003; Franks, Lyn, Klein, & Reiss, 2009). Due to the uncertainty of interpreting stereotypical behavioral patterns, additional measures should be included in order to determine the overall health of an animal that is engaging in such behavior (Mason & Latham, 2004).

In the current study, circle swimming increased for all three dolphins during the post-introduction period, but the increase was much higher for Chance, the new individual, compared to Bo and Buster, where the increase was negligible. Circle-swims increased from 40% of Chance's swim behavior during baseline to 90% of his repertoire during the post-introduction phase. For group members Bo and Buster, the repertoire of swim behavior remained almost identical during the baseline and post-introduction phases. In addition, although dolphin enrichment devices, more commonly referred to as "toys", were nearly always present, the new individual, Chance, all but ceased interacting with the enrichment objects during the post-introduction phase. Animals that are under stress typically do not interact with enrichment devices (Fraser & Duncan, 1998; Held & Spinka, 2011; Spinka, Newberry, & Bekoff, 2001). Alternately, object play and circle swimming increased slightly for group members, Bo and Buster, during the post-

introduction phase. Taken together, these behavioral changes indicate that the experience was stressful for Chance but may have caused excitement or agitation for Bo and Buster.

Bo and Buster – Heightened states of arousal

Stress hormones are also responsible for heightened states of arousal such as excitement, anxiety, agitation, frustration, or fear (Sapolsky, 1998). Based on the increase in circle swimming, object play, and signature whistling, it is likely that Bo and Buster were experiencing a heightened state of arousal that could have included one or more of these states. Animals responses to stress and the specific state of arousal that results is determined by multiple factors (Fanselow & Lester, 1988; Rau & Fanselow, 2007). However, members of a species typically respond to specific stimuli in a similar way (Bolles, 1970). For example, in captivity, dolphins typically respond to fear by quickly forming a cohesive group (Bel'kovich, 1991; McBride & Hebb, 1948; Tavolga, 1966). Prior to this study, Bo and Buster had been observed reacting in this way when novel enrichment objects were added to their pool (Lyn et al., in review). When Chance was first introduced, Bo and Buster did not exhibit a fear response, as they were engaging in different swim patterns following the introduction.

Bo's swim patterns and spy hopping behavior at the time of the initial introduction was consistent with behavioral patterns described as anticipatory (Jensen, Delfour, & Carter, 2013). Jensen et al. (2013) found that as feeding time grew near, dolphins tended to engage in more spy hopping behavior and activity levels decreased. Bo could have been engaging in these types of behaviors when Chance was introduced because of the presence of trainers near the pool. However, she continued these behaviors one and a half hours after the initial introduction when trainers were no longer present.

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Since the introduction of a new dolphin was an uncommon situation and the individual being introduced was new, the behaviors exhibited by Bo could be interpreted as excitement instead of anticipation.

Buster also exhibited high energy behaviors as Chance was added to the pool just before he began continuous circle swimming. Circle-swimming may also be linked to anticipatory or excited behavior (Gygax, 1993). This swim pattern was also sustained during the session following the initial introduction. Although Buster frequently engaged in circle swimming during the baseline phase, there was an increase in circle swimming for all three dolphins during the post-introduction phase indicating that the increase in circle swimming may have been due to heightened states of arousal for all three animals.

<div align="center">A typical introduction?</div>

As with many behavioral studies, there were many variables that could have affected the behavior of the dolphins and the vocalizations produced during this study. Therefore, the findings presented here may or may not be typical of bottlenose dolphin introductions. Although there are very few instances of dolphin introductions in the published literature, in many ways, the behavior of Bo, Buster, and Chance differed from these reports. Published accounts of primate, specifically chimpanzee and gorilla, introductions are more abundant. Both of these species, but chimpanzees in particular, are highly social and exhibit high rates of agonistic behaviors that are similar to dolphins. As a result, comparisons can be made between these species regarding the behaviors observed during introductions.

Typical subjects?

First, the subjects involved in this study varied in age, with two of the dolphins in their 30's, while Chance, the new individual, was predicted to be less than six years of age. The sensory capabilities of the older dolphins were unknown, so it was possible that they may have had age-related eyesight or hearing impairments. Chance may have also suffered from an unknown impairment that was not apparent. Based on medical examinations, Chance was known to have a slight spinal deformation. There may also have been other unknown impairments due to the circumstances surrounding his stranding and rehabilitation.

Many times young dolphins are often found stranded alone without their mother (Wilkinson & Worthy, 1999). This is not ideal because calves learn how to obtain food, avoid threats, and navigate the complexities of dolphin society from their mothers (Gibson & Mann, 2008). Dolphins that are found stranded and are younger than two years of age are typically deemed non-releasable and remain in captivity because they are unlikely to have learned enough to survive alone in the wild (Moore et al., 2007; Noren & Edwards, 2007; Whaley & Borkowski, 2009). Thus, young stranded dolphins may not be typical in terms of their knowledge of survival or social skills. In addition, they may also be suffering from sensory or cognitive deficits that could impact their ability to interact normally with other dolphins.

Once rescued, stranded dolphins are typically held isolated in quarantine. It is unknown exactly how isolation can affect the development of a young animal, and the impact is likely different for each individual (Janik & Sayigh, 2013). Chance was held in isolation for 11 months prior to his introduction to Bo and Buster. It is possible that his

cognitive, social, or auditory development may have been altered due to this experience. This could have also impacted his communicative abilities relating to vocal production. For example, very young stranded dolphins have been reported to "lose" their signature whistle while in isolation (Caldwell et al., 1990). This did not appear to be the case for Chance because his signature whistle dominated the baseline recordings and was also observed in all other phases of the study. Based on the behavioral observations, there was no indication that Chance's behavior was abnormal and during training sessions with Chance, animal care staff reported no behavioral abnormalities that would indicate a cognitive impairment. Other variables, such as personality (Highfill & Kuczaj II, 2007), past history, or hormonal changes due to the time of year the study was conducted could have also influenced the behavior of dolphins during integration. Even considering all of these variables, it is still highly likely that there is a range of standard behavioral responses, including vocal responses, to specific social contexts such as an introduction.

Typical in the literature?

Bottlenose dolphins are well known for their aggressive interactions both in captivity and in the wild (Lockyer, 1990; Norris, 1967; Patterson et al., 1998). In the literature, agonistic behavior is commonly reported to occur during dolphin introductions (McBride, 1940; McBride & Hebb, 1948). Juvenile dolphins seem to be involved in more conflicts than animals of other age classes, with higher rates of agonism reported for juveniles of both sexes (McBride, 1940; McBride & Hebb, 1948; Norris, 1967; Samuels & Gifford, 1997; Tavolga, 1966; Weaver, 2003). Young males in particular have been reported to receive negative attention from older more dominant males in the form of outright attacks, especially if the younger male shows interest in the females, or in the

form of sexual attention with the younger male playing the "female role" (McBride & Hebb, 1948; Tavolga, 1966; Tavolga & Essapian, 1957). Based on this information, it was assumed that at least some aggressive interactions would occur during this study, particularly between Buster, an adult male, and Chance, the juvenile male being introduced. However, no visible signs of aggression were observed even when Buster was physically introduced to Chance. These findings were surprising and may indicate that factors like individual differences in personality are more important than age and typical dominance interactions in predicting aggressive behavior during an introduction. Many animals, including dolphins, have been shown to have distinct personalities, meaning that there are individual differences in behavioral responses to certain situations and these responses are stable over time (Highfill & Kuczaj II, 2007; Kuczaj II, Highfill, & Byerly, 2012).

Although predominantly aggressive interactions during dolphin introductions are common in the early literature, these few reports may not be representative of the typical dolphin introduction. These reports are anecdotal in nature and do not provide an account of every introduction. It is possible that uneventful introductions were not mentioned because they were commonplace or believed to be unimportant. Also, the aggressive behavior observed during these early accounts is not limited to an introduction context. It can occur during many contexts including any time there is a shift in the dominance hierarchy of a group (Frohoff, 2004; Norris, 1967; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005; Waples & Gales, 2002).

It should also be noted that many of the descriptions are from a period when the marine park industry was still in its infancy. These publications describing group

introductions also contain some of the first reports of dolphin behavior, including courtship behavior, sexual behavior, and birthing. Since that time, knowledge of dolphin behavior and husbandry practices has increased exponentially and captive populations are now managed by highly trained staff, including trainers and veterinarians who rely on years of combined experience to carefully monitor social interactions and intervene when necessary. Husbandry practices involving other species have undergone similar evolutions (Seres, Aureli, & de Waal, 2001).

There is only one quantitative report describing dolphin vocalizations during and introduction. An honor's thesis from the University of Southern Mississippi (USM) looked at vocalizations during the physical introduction of a new dolphin into an existing group (Brady, 2015). In this thesis, production of whistles, burst-pulses, and other vocalizations were analyzed from audio recordings, totaling four hours. The amount of time between the initial introduction and the onset of data collection was not specified. Baseline recordings were not collected for the new individual prior to it being introduced into a holding area where it was physically but not acoustically isolated from the group. The study did not include collection of behavioral data or analysis of signature whistles. Due to the lack of baseline data for the new individual and the brevity of the recordings, the results of this honor's thesis were not directly comparable to the results presented here.

Typical across species?

Like dolphin introductions, aggression and even mortality can occur during primate introductions and these outcomes can also occur whenever there is a shift in the dominance hierarchy of the group (Abelló & Colell, 2009; Brent, Kessel, & Barrera,

1997; McBride, 1940; Waples & Gales, 2002). Relatively few studies have provided quantitative accounts of introductions involving primates, and the introduction process that is commonly used is similar to the one that was used to introduce Chance to Bo and Buster. In many cases, animals are allowed visual and auditory contact before being physically introduced, and brief, one-on-one physical introductions take place across multiple sessions before permanent group integration takes place (Abelló & Colell, 2009; Brent et al., 1997; Jacobs et al., 2014; Schel et al., 2013; Seres et al., 2001).

The outcomes of chimpanzee introductions are also similar to those reported for dolphins. In one study involving 165 chimpanzee introductions, most integrations were successful, even when agonistic interactions were initially observed (Brent et al., 1997). Acceptance or group stabilization usually occurred within one month of introduction and if intervention was needed, it almost always occurred within one month (Brent et al., 1997). For Chance, Bo, and Buster, the sudden drop in signature whistling on the day of introduction and the recovery of signature whistle rates that occurred during the following phases indicates acclimation occurred within one month following the day of introduction. It is unknown how permanent physical integration would have affected acclimation but it is possible that more aggression would have been observed.

What does this tell us about wild dolphin behavior?

Although this study describes signature whistle production before the dolphins were physically introduced on a long-term basis, in some ways, this may be more akin to how introductions would happen in a wild setting. Keeping the dolphins physically separated allows the introduction to occur more slowly and prevents the immediate need to establish dominance as soon as the new individual is introduced. In the wild,

introductions do not occur in a confined setting; therefore, in most cases, individuals do not have to remain in one another's presence for extended periods of time unless they choose to do so, or are forced to do so such as during courtship (Connor, Smolker, & Richards, 1992). In the wild, threat displays may result in the subordinate dolphin leaving the vicinity without experiencing direct sustained violence, although aggression resulting in bodily injury is common (Norris, 1967; Scott et al., 2005). Since direct violence is not possible in a captive introduction in which the animals are physically separated, vocal threat displays and vocal communication in general would be expected.

Buster's whistle rate remained relatively steady and a slight increase in circle swimming was the only real behavioral change seen after introduction. Buster whistled more than Bo during the baseline phase and his whistle rate increased only slightly following an increase in novel whistles in his environment. One possible reason is that Buster could have been indifferent to the addition of Chance. Since Chance was physically isolated in an area of the pool where Buster did not frequent, Buster may have viewed his presence as inconsequential. It is also possible that Buster's behavior was a form of stereotypy or that circle swimming was his preferred sleep style (Sekiguchi & Kohshima, 2003) and this contributed to the appearance of excessive circle swimming. An alternate possibility is that Buster's steady swim behavior and whistle rate acted as a sort of patrolling behavior (Clark, 2013), swimming the boundary of his territory and calling out to let others know of his presence. Adult male dolphins have large, overlapping territories and socialize with fewer individuals than females (Randic, Connor, Sherwin, & Krutzen, 2012; Smolker et al., 1992). Whistles can be transmitted up to 25 km underwater (Janik, 2000a), depending on whistle source levels and

environmental conditions, so a traveling male would need to whistle infrequently in order to alert others of his presence. Vocal territorial announcements are common among many species as they aid in avoiding direct conflict that could result in injury, weakness, and loss of status (Huntingford & Turner, 1987; Norris, 1967). The vocal behavior of adult males in the wild is largely unknown (Watwood et al., 2004), but like other species, the acoustic properties of dolphin vocalizations are likely distinctive, potentially transmitting information about size and sex (McIntosh, Dudzinski, & Mercado, 2015).

Bo's abrupt increase in whistling following the introduction of Chance, paired with her change in behavior and interest in Chance on the day of introduction indicates that she was aware of Chance's presence and may have been attempting to communicate with him. Excluding Bo's whistle, there were fewer whistles produced in the main pool on the day of introduction compared to during baseline, meaning Bo's increased whistle rate was not due to being exposed to an increase in whistles in her environment. However, exposure to novel whistles could have caused her to whistle more and also to approach Chance. Several studies have found that dolphins respond to whistles by whistling back (King et al., 2013; Lang & Smith, 1965; Nakahara & Miyazaki, 2011) and that they may also respond by approaching the dolphin that is whistling (Caldwell et al., 1990). Bo's vocal behavior and interest in Chance seemed to coincide with the finding that wild dolphins meeting at sea produce signature whistles before coalescing (Quick & Janik, 2012).

<center>Sources of Error</center>

The ability to localize the source of dolphin vocalizations is key to determining specific vocal interactions. Localization would allow for the detection of whistle

<center>65</center>

matching events, which could signal acceptance by group members or some other type of significant social milestone. In this study, localization was not possible for the majority of whistles observed for several reasons. First, Chance, the new individual who was confined to the area inside of the array, produced very faint whistles that were typically detected on only one channel even when whistles produced by the dolphins outside of the array were visible on two to three channels. In addition, the background noise in the pool combined with the occasional distortion created from the hydrophone cables masked the lower frequencies of some whistles, most of which were characterized by a low signal-to-noise ratio. Underwater concrete pillars that supported the dock system and framed the inner array area may have also blocked some signals from reaching multiple hydrophones. Reflection from pool surfaces, the direction of sound emission, and the degree of tonal modulation of the whistle also may have affected the ability to localize. These factors, as well as the loss of sound energy in key parts of the whistle containing distinctive features, may have also contributed to the low ratings of some whistles during classification.

Because the dolphin producing each whistle was unknown in almost all cases, the signature whistles observed could have originated from the whistle owner or could be whistle copies that originated from a different dolphin. Signature whistle copying is rarely observed (Janik & Sayigh, 2013), so it can be assumed that the majority of the signature whistles observed were produced by the whistle's owner. However, localization results indicated that, in at least one case, Bo produced a copy of Buster's signature whistle.

Conclusion

Only one study has looked at the role of signature whistles in wild dolphin introductions. Quick et al. (2012) found that dolphins meeting at sea exchange signature whistles before inter-mixing. Signature whistle exchange occurred between Bo, Buster, and Chance, but the exchange did not occur as expected. The new individual, Chance, did produce some signature whistles as soon as he was introduced, but he did so at much lower rates compared to any other study phase. Stress is the most probable reason for the decline in whistling, but this response may not be characteristic of all dolphins, as dolphins experiencing isolation and stress often produce whistles at higher rates (Esch, Sayigh, Blum, et al., 2009). The whistle rates of the adult male, Buster, did not change significantly, but the rates for the adult female, Bo, increased following introduction. Bo also showed more interest in Chance on the day of introduction. There are many possible reasons for Bo's reaction such as individual personality or maternal instinct (Kuczaj II et al., 2012).

Acclimation occurred within one month following the initial introduction and was characterized by the recovery of signature whistle rates. Acclimation or failure to acclimate within a one-month period coincides with reports from other studies involving dolphins (McBride, 1940; Samuels & Gifford, 1997) and chimpanzees (Brent et al., 1997; Seres et al., 2001). Aggression during dolphin introductions is commonly reported in the early literature, but in this study, no aggression was observed even when animals were physically introduced to one another. Because there are no large-scale quantitative assessments of behavior during bottlenose dolphin introductions, typical levels of aggression during introductions are unknown.

Age, individual histories, personality, sex, and group composition may all be factors that influence behavior and signature whistle production during an introduction. Analysis of additional dolphin introductions with an array of group compositions is needed to determine typical dolphin behavior, including the production of signature whistles, in the context of dolphin introductions. Localization of whistles would be extremely important in assessing the fine scale interactions between individuals in this context. Further research conducted in a controlled setting may allow us to relate these findings to wild dolphin groups in similar situations and will help us to interpret vocalizations used in those contexts.

APPENDIX A - Localization Calibration

Localization accuracy and error (calibration) were assessed by localizing sounds produced at known locations. Calibration sounds were produced by tapping a pair of dive weights together approximately 12 cm below the surface of the water at 36 locations around the main pool (Figure A2). Localization in TOADy was considered successful if at least three intersecting parabolas were produced. The location of the intersection of three or more parabolas was considered the predicted sound source location. Error was approximated by estimating the distance in meters between the known sound source and the center of the triangulated region created by the intersecting parabolas.
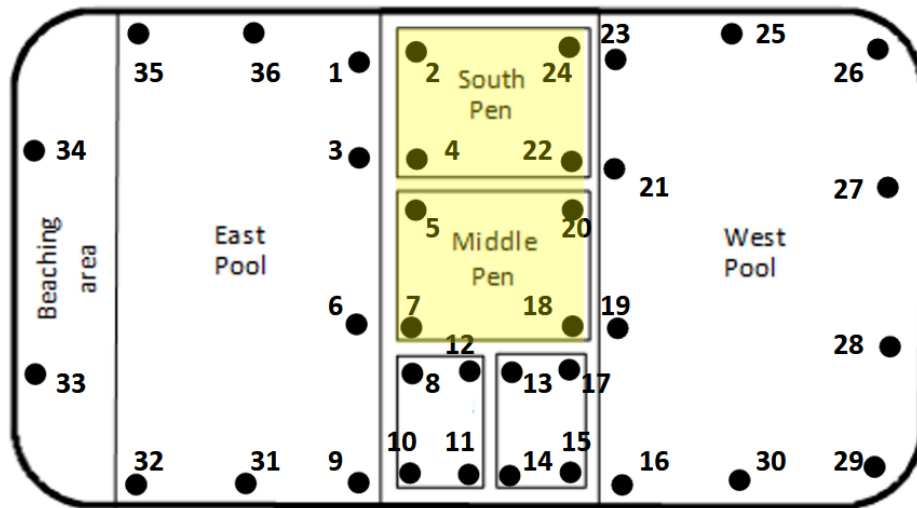
Figure A1. Test Calibration Locations.

Calibration locations in the main pool. Each location is marked and numbered. Calibration sounds were produced at each location by tapping a pair of dive weights together approximately 12 cm below the surface of the water. The area in yellow represents the area inside of the hydrophone array. This area was occupied by the new individual Chance.

Whistles recorded during the study were classified as 1) originating from the area occupied by the group, Bo and Buster, 2) originating from the area occupied by the new individual, Chance, or 3) "unknown" if the origin of the sound source was ambiguous or

impossible to localize. Localization was considered successful and unambiguous if the program produced at least three parabolas that overlapped to create a triangular area that was located fully inside or outside of the hydrophone array.

Calibration Results

Localization was possible for ten of the 36 calibration points (Figure A1, Table A1), with six of those ten points localized to the correct area, either inside or outside of the array, and an estimated error ranging from 0-7 m away from the exact location of the sound source (Figure A1). Five out of six of the correctly localized points originated from inside the array, while all four incorrectly localized points originated from outside of the array (with the localization results placing the sound source inside the array). The four incorrectly localized points also had larger errors (ranging from $7 - 14$ m) than the correct points. Only one out of five calibration sounds that originated from outside of the array was successfully and accurately localized whereas all five points that originated from inside the array were successfully and accurately localized. In all, localization was far more accurate for sound sources that originated from inside the array; although, there was also a high rate of false positive localizations to the inner array area.
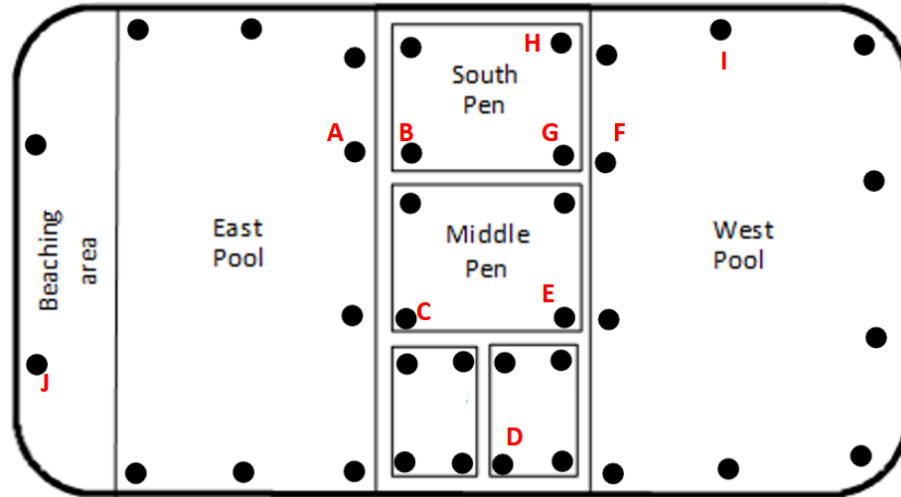
Figure A2. Successful localizations during calibration.

Localization sound calibration locations represented by black dots. Labeled points represent the calibration sounds that were able to be localized. The points correspond to those used in Table A1 and Figure A2.

Table A1.

Results for calibration sounds for ten locations labeled A-J.

		Location of Origin	Localization Results	Estimated Error
A	-	Outside	Outside*	2 m
B	-	Inside	Inside	0 m
C	-	Inside	Inside	7 m
D		Outside	Inside	10 m
E	-	Inside	Inside	4 m
F		Outside	Inside	7 m
G	-	Inside	Inside	2 m
H	-	Inside	Inside	4 m
I		Outside	Inside*	12 m
J		Outside	Inside	14 m

The labels correspond to those used in Figure A1 and A2. Dashes next to each letter indicate cases were the localization results were accurate. Asterisks indicate locations were the predicted area was not fully located inside of the zone reported

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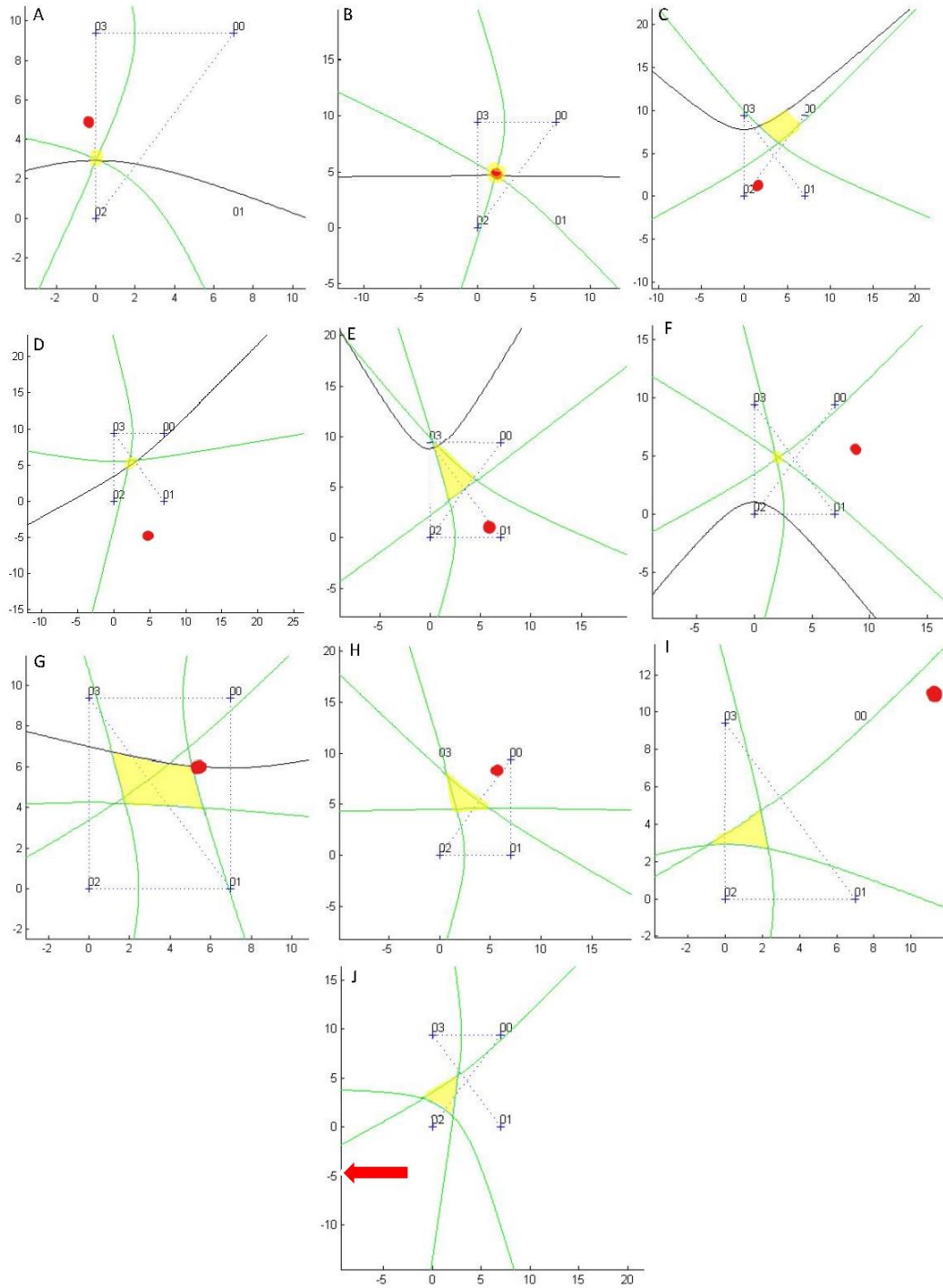Figure A3. Results of calibration for ten locations labeled A-J.

The hydrophone array is represented by the rectangle created by the four points labeled 00-03. The location of the sound source is indicated by the red dots and the red arrow in diagram J. Localization parabolas are represented by the solid black and green lines. The yellow area in each diagram is the predicted location of the sound source.

Sources of Error

Only one third of the calibration points were successfully localized and six out of ten of those calibration points were correctly assigned to the area of the pool in which the test sound originated. Of the ten localized sounds, all five sounds originating from inside the hydrophone array were localized accurately with error estimates ranging from 0 to 7 m. Only one of the five sounds originating from outside the array was localized accurately. The inaccurate localizations had errors ranging from 7 - 14 m and they all suffered from the same bias in that they originated from outside of the array but were incorrectly classified as having originated from inside of the array. This means that, although most localizations that predicted that a sound originated from inside of the array were accurate, there were also many false positives intermixed with the accurate predictions. Thus, localization predictions that indicate a whistle originated from inside of the array should not be relied upon. On the other hand, since all sounds originating from inside the array were correctly localized, there is much less of a chance that whistles originating from inside the array would be localized to other pool areas. Since sounds originating from inside of the array were always localized to the correct location, localization predictions that indicate a sound originated from outside of the array have a much higher chance of being accurate as no false positives in this direction were observed during calibration.

Several factors could have contributed to these results. First, it is highly possible that the acoustic properties of the pool, along with the specific location and the nature of the sound, which was more similar to echolocation clicks than whistles, created

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reflections within the pool. Reflections occur when sound waves bounce off the surfaces in the pool and continue to travel in a different direction. These reflections are recorded by the hydrophones and can lead to errors when trying to localize because they act as an additional simultaneous sound source originating from a different direction thus causing interference.

Second, dive weights were used to create the calibration sounds instead of dolphin whistles. Ideally, the localization calibration would have been conducted using both the short-duration, broadband clicks of the dive weights as well as narrow-band, frequency modulated sound types that were similar to the dolphin whistles localized in the actual study. The dive weights used for calibration were short-duration broadband signals that were similar to the echolocation clicks of dolphins. Echolocation clicks are easier to localize because they are high-energy sounds and the onset of the signal is typically well defined. Whistles are generally more difficult to localize because the duration of the signal is longer and the sound energy is more spread out. As a result, there may not be a clear cross-correlational peak to localize, and the onset of the signal may not be captured on all hydrophones. However, these limitations can be overcome when whistles have a high signal to noise ratio and a high degree of frequency modulation. During calibration, the high energy clicks of the dive weights may have traveled farther than lower energy whistles and resulted in more reflections off of the surfaces of the pool. In addition, the clicks produced by the dive weights were short duration, low frequency sounds with a frequency range of $0 - 3+$ kHz (Figure A3). Due to the low frequency of the sounds, they were often obscured by noise, which made localization difficult.
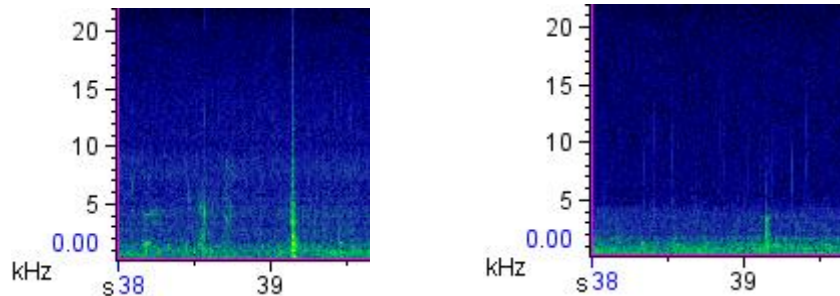
Figure A4. Spectrogram of dive weight clicks.

Spectrogram images of the sound produced by clicking two dive weights together underwater used for localization calibration. Each image shows the same sound as it was detected on two different hydrophone channels.

Unfortunately, whistles could not be used for the calibration because it would have required the use of an underwater speaker to playback pre-recorded whistles into the main pool while the dolphins were present. This procedure would have required additional permitting and approval from IMMS that was not able to be obtained. Another option would have been to have one of the resident dolphins produce an underwater whistle under the direction of a trainer. Again, this would have required approval from IMMS staff that was not able to be obtained. Also, there would be several drawbacks to this method. The dolphin used for the test would have to be able to reliably produce whistles on cue and there would be no way to verify that whistles were reliably produced by the test dolphin. There would also be no way to determine if the test dolphin produced the whistle or if a whistle was produced by another dolphin in the pool at the same time. Lastly, the dolphins at IMMS do not typically perform this behavior during training sessions. It is also extremely difficult for trainers to confirm if the whistle was produced underwater, as there are no behavioral cues that can be seen by the trainer, and the sound, if it could be heard in air, would be very faint and likely masked by noise.

During the calibration, only three of the four hydrophones were functioning properly. The hydrophone that malfunctioned produced faint recordings with low signal to noise ratio. This channel was still suitable to some degree and was used during localization. It is unknown if the use of this channel resulted in the high rate of error for signals originating from outside of the array. If this channel had been functioning properly as it was for the actual study, the localization results from the calibration test may have been more accurate.

APPENDIX B - Signature Whistle Determination

Out-of-Water Recordings

Buster's whistle was determined by analyzing previously recorded, in-air

vocalizations collected when Bo and Buster were transported to IMMS in 2011. These

recordings were collected with support from IMMS staff and were recorded using a

Zoom H1 handheld audio recorder (sampling rate 48 kHz, 24-bit resolution) or a Canon

VIXIA HF100 handheld video recorder (sampling rate 48 kHz, 16-bit resolution). The

Zoom H1 recorder settings allowed for recordings to be produced in a .WAV file format.

Recordings from the Canon HF100 produced .MTS video files. The video files were

converted into .WAV files using Smart Converter for Windows by Shedworx.

Conversion of Compressed Files

Because the compressed video files had to be converted into an uncompressed

format for analysis, both the ZOOM H1 audio recorder and the Canon video camera were

used to simultaneously record a dolphin whistling in-air at the request of a trainer during

a training session. This was done to determine if the conversion process altered

identifying features of the signal, such as the shape of the contour or the frequency. The

file produced by the Canon HF100 was converted to a .WAV file using Smart Converter

and compared to the Zoom H1 .WAV file using Raven. The converted file resulted in a

reduction of the clarity of the signal but the shape of the contour and frequencies were

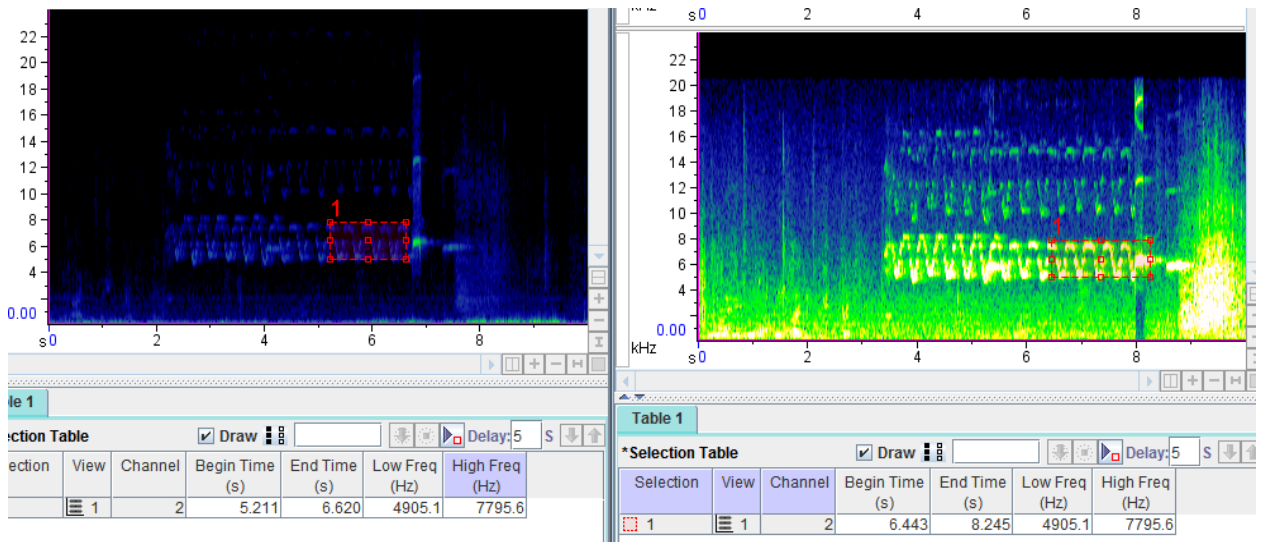consistent with the unconverted .WAV file (Figure B1).

Figure A5. Simultaneous whistles.

Spectrograms of simultaneous recordings from a .WAV file from a Zoom H1 recorder (left) and a .MTS video file that has been converted into a .WAV file (right).

Simple Categorization

The simple categorization method was used to categorize all whistles and to determine the signature whistle for each dolphin. This method was used to classify out-of-water recordings collected from Buster, recordings from Chance while he was isolated during the baseline phase, and also for the rest of the dataset. Each set of recordings was treated as a separate dataset. For each dataset, M.B. sorted whistle contours into categories for each unique whistle type observed. Whistles were classified into major and subcategories based on the most prominent features of the contour. Major categories and descriptions are listed in Table B1. Subcategories included variations within each major category that had a similar contour and frequency range. Each major category contained multiple subcategories. The predominant whistle sub-type observed for each set of data was deemed a signature whistle.

Table A2. *Major category types and description of whistles in each category.*

Major Category	Description
Positive Slope	Most prominent feature is a positive slope
Negative Slope	Most prominent feature is a negative slope
Sine	Most prominent feature includes a full or partial sine wave
Flat	Most prominent feature includes an area with no frequency modulation
Other	Contours with multiple or no prominent features

Classification by Naïve Raters

A test of inter-observer agreement was required to determine if signature whistle classifications made by M.B. using the simple classification method could be used for analysis of the full dataset. This was achieved by conducting a test of inter-rater reliability comparing the ratings of M.B. and those of five naïve observers on a set of 119 whistles chosen as "training data" and as well as a randomly chosen subset of 20% of whistles from the full dataset.

One major difference between the naïve rater method and the simple classification method is that the simple classification method was an iterative process where one observer categorized all whistles in a dataset without comparing whistles to any known exemplars. Whistle types were created, combined, or fragmented based on the experience of the observer as they sorted through the whistles. The naïve rater method involved raters comparing each whistle to a catalog of known exemplars and they did not create or decide on new categories of whistles.

Exemplars

To begin, M.B. chose one or more spectrograms to be used as exemplars of each dolphin's signature whistle. Spectrograms were chosen that clearly demonstrated the most commonly observed, complete version of each dolphin's signature whistle available

based on the results of the simple classification method. Two of the dolphins had signature whistles that often consisted of multiple loops. For these whistle types, multiple spectrograms were chosen to illustrate the varying number of loops and/or varying forms of common pre or post loop elements.

Raters

Five raters were chosen to rate the similarity of each whistle to the exemplars. One rater had previous experience with bottlenose dolphin whistle classification but the others had no experience with acoustic analysis of any kind. All raters remained naïve to the phase of the study, the individual producing the whistle and the owner of each signature whistle exemplar or exemplar set. In addition, raters never assisted one another nor did they view the rating scores of one another over the course of the project. Prior to being given the rating task, inexperienced raters were given a familiarization task that involved carefully viewing each whistle in the dataset. This was done so that they would begin to recognize similarities and differences between whistles, and would begin to recognize common whistle types outside of the context of rating whistle similarity.

Distinguishing Features

After the familiarization tasks were complete, raters were given spectrogram images of each exemplar or exemplar set and were asked to locate what they would consider to be distinguishing features for each exemplar. This task was also completed by M.B. who was aware of the study phase and the whistle owner. The distinguishing features that were agreed upon by all five raters and M.B. were combined and transferred onto the exemplar images by circling or drawing arrows to each feature using the photo editing and drawing feature on a Surface Pro 2 computer with stylus pen. Contour

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drawings of each exemplar were created using the same software. A whistle catalog was created that contained the distinguishing features diagrams, contour drawings, and additional exemplar images, as well as a verbal description of the exemplar title, shape, distinguishing features, presence or absence of loops, loop description, and other common features (see Appendix C).

Rating Instructions

An additional rating instructional document was created to provide raters with a basic level of understanding of the terminology and best practices commonly used when working with dolphin acoustical data, as well as the rating scale to be used for this study and operational definitions for key qualifiers in the rating scale (Appendix D). Raters were given both documents to review and were instructed to first, determine which exemplar in the catalog most closely resembled each whistle in the data set. Once an exemplar match was chosen, raters were asked to rate the similarity of that whistle to the exemplar using the rating scale provided (Table B2).

Table A3.

Rating scale.

Rating	Description
1	In no way similar in shape to the exemplar
2	Has some features in common with exemplar
3	Has most (~75%) features or a distinguishing feature in common with the exemplar
4	Frequency and a distinguishing feature of exemplar matches but is not an exact copy
5	Almost exact duplicate of exemplar in terms of frequency and shape

Rating scale used by independent raters to specify the level of similarity between a whistle and the exemplar.

Training

In order to assess if enough information had been provided, raters were asked to use the instructional documents to rate a sample of 119 whistles chosen from the full dataset. Whistles in the dataset where chosen so that there were non-signature whistles and multiple variations of each dolphin's signature whistle, including odd formations, partial whistles, and those that varied in loop number. M.B. also completed this rating task and her ratings were included in the tests of inter-observer agreement. Inter-rater reliability for template choice was very high (Fleiss' kappa = .84) and agreement on scores was acceptable (Krippendorff's alpha = .65) indicating that the information provided in the rating instructions and whistle catalog were adequate and raters could proceed with rating a larger subset of the data. In all, 42% of the whistles in the training set matched Chance's signature whistle, 17% matched Bo's whistle, and 10% matched Buster's whistle.

Inter-rater Reliability

After completing ratings for the training set, raters were asked to rate a subset of 20% of whistles (n=1068) that were randomly chosen from the entire dataset. M.B. also completed this task and her ratings were included in the tests of inter-rater reliability. Inter-rater reliability for template choice (Fleiss' kappa = .87) and scores (Krippendorff's alpha = .94) were very high indicating that M.B.'s ratings were reliable and could be used for analysis of the full dataset. Of the subset of 1068 whistles that were randomly chosen to be rated, 69% matched Chance's whistle, 3% matched Buster's whistle, and 4% matched Bo's whistle. The actual number of whistles are presented in Table B3.

Table A4.

Signature whistle template matches.

	Chance	Bo	Buster
All Template Matches	855	59	154
Rated 3 and higher	735	34	40

Signature whistle template matches and matches with ratings of ≥ 3 from the 20% subset of whistles that were rated by naïve raters.

Signature Whistle Analysis

Whistles that were rated three or higher in similarity to an exemplar from the catalog were considered a signature whistle match. Only signature whistles that met these criteria were used in signature whistle analysis. Partial whistles with a rating of two were labeled as probable or possible signature whistles if the contour and frequency of the partial whistle matched the exemplar. Buster's whistle was a very common whistle type in that it had a positive slope. Therefore, partial whistles that were similar Buster's signature whistle may or may not have been matches even though the partial contour shape and frequencies matched Buster's whistle exactly. Because of this, partial whistles matching Buster's exemplar were labeled as possible instead of probable signature whistles. In the analyses, probable and possible whistles were included in counts of "other" whistles types.
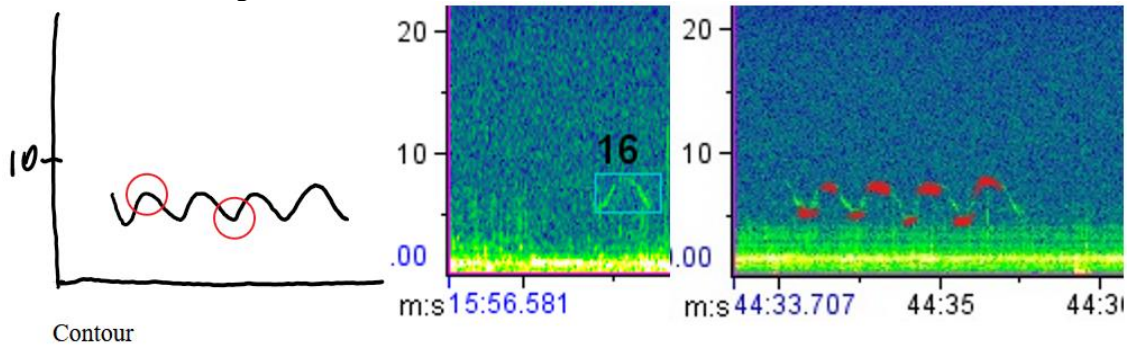
Exemplar C
- Shape: Parabola
- Distinguishing features (marked in red): There is only one, it is the top curve of the parabola.
- Loops are rare. This whistle usually appears as a single whistle.
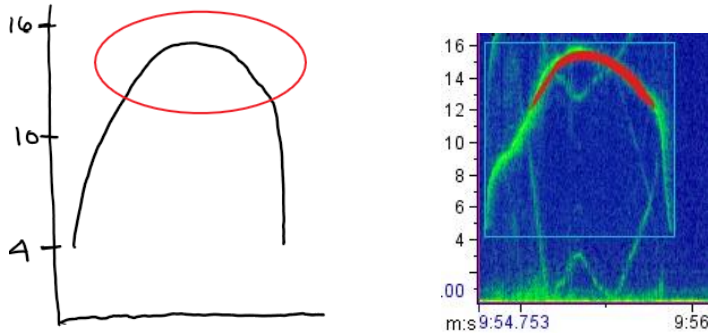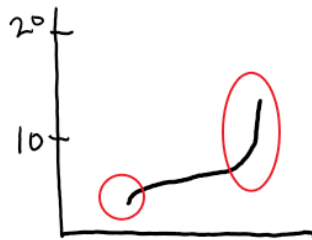

Contour

Exemplar O
- Shape: Sin Wave
- Distinguishing features - There are two, a bottom trough and top peak of the wave.
- Loops are common, usually connected with 3-4 loops. However, it can appear as a single whistle as in the image below where the top peak of the wave is visible OR with the bottom trough visible.

Contour

Exemplar U

- Shape: Upsweep
- Distinguishing features: There are two, a bottom curve and top curve
- Loops are common but appear <50% of the time. If there are loops, they are disconnected.
- The distinguishing loop usually appears last in the set and the distinguishing features of the whistle are the downward curve at the beginning and the upward curve at the end of the distinguishing loop. These can be very difficult to detect so look for slight differences.

Contour for
Distinguishing Loop
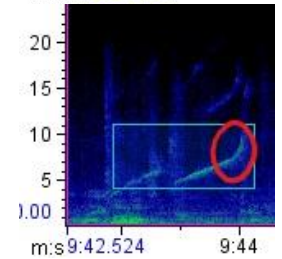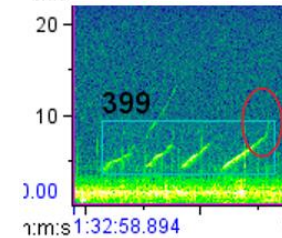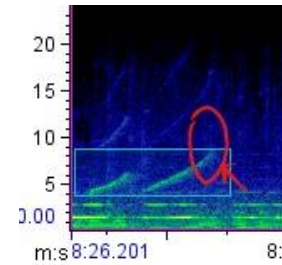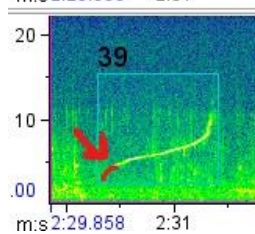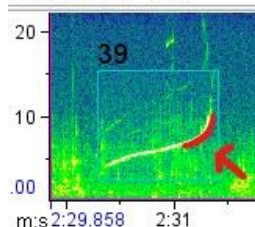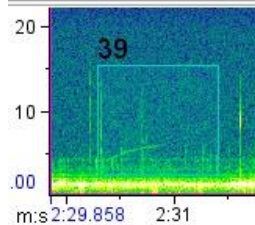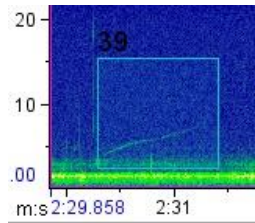
APPENDIX D – Rater Instructions

Terminology

Exemplar – Each whistle type within the whistle catalog (Appendix C) is an exemplar.

Spectrogram - The graph which depicts the whistles with frequency shown on the y-axis and time on the x-axis.

Frequency Contour - The shape of the whistle. More specifically, the change in frequency with time. a.k.a. the whistle, the signal

Fundamental Frequency Contour - The contour present at the lowest frequency. a.k.a. the whistle, the signal. Repetitions at higher frequencies are known as harmonics. When comparing whistles to the exemplars, ignore the harmonics.

Whistle - One sound unit. Can consist of one or more connected or disconnected loops. Each box in the chart below (Figure D1) depicts one whistle. One whistle can have multiple parts or loops and may vary in duration.

Loop - A *repeated* contour or contour part that occurs within .5 sec. of one another. The beginning or ending loop in a series may be different than the interior loops (ex. FB90, FB97 in Figure D1). The number of loops can vary depending on the emotional state of the dolphin.

Inflection point - the point in the whistle contour where the slope of the contour changes or curves. Whistles commonly have multiple, distinctive inflection points.
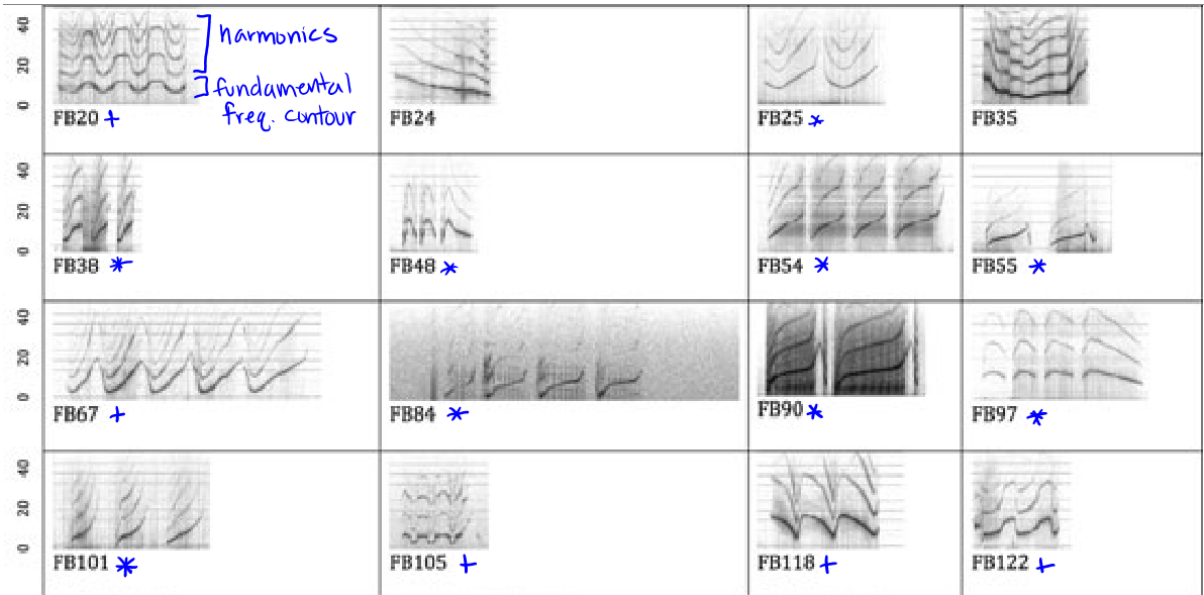
Figure A6. Modified table presented in Esch et al., 2009

+Whistle with connected loops

*Whistle with disconnected loops

Table A4. *Rating Scale*

Rating	Description
1	In no way similar in shape to the exemplar
2	Has some features in common with exemplar
3	Has most (~75%) features or a distinguishing feature in common with the exemplar
4	Frequency and a distinguishing feature of exemplar matches but is not an exact copy
5	Almost exact duplicate of exemplar in terms of frequency and shape

Features to consider when assessing similarity

- Overall shape

    - Includes minimum and maximum frequency and location of peaks and

      inflection points.

- Minimum and Maximum frequency

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- Use the frequency parameters as a guide. They do not have to be exact, especially for partial whistles. If the signal strength is weak, the start and end points of the whistle may not be visible. Therefore, the minimum and maximum frequencies may not match the exemplar even though other features do match. Take this into consideration when assessing similarity

- If the shape is similar but the frequency does not match when you mentally overlay the contours, then the whistle should not be rated as similar.

- Duration
  - The duration or length of a whistle should not be considered when you are rating a whistle. Look at overall shape and the frequency but be sure to take into account partial whistles and whistles that appear across multiple channels (below).

- Loops
  - For a multi-loop exemplar, whistles can have more or less than the number of loops present in the exemplar without negatively affecting the similarity rating.

- Partial Whistles
  - What is a partial whistle? Each part of a whistle may not be produced with a uniform intensity or loudness. As a result, certain parts of a whistle may not appear on the spectrogram. This could be due to the way an animal produces a whistle or whistle type, the direction an animal is swimming, changes in direction when swimming, or other factors. It is common for the beginning or

ending of a whistle to be faded or missing. You may also see breaks in a

whistle.

- ○ Partial signature whistles sometimes occur. A partial whistle can receive a
  rating of 3 or higher only if the visible frequencies of the contour match the
  exemplar and more than 75% of the whistle matches the exemplar OR if key
  distinguishing features are present (such as inflection points). Distinguishing
  features are marked in the whistle catalog.

- ○ Multi-loop whistles with differing pre or post loop elements - For a partial
  whistle to receive a rating of 3 or higher, it must, without a doubt, match one
  of the exemplar loop elements.

- ○ To determine if a suspected partial whistle matches the exemplar, mentally
  overlay the partial whistle contour over the exemplar. Then rate the similarity
  of the whistle to the exemplar based on the rating scale.

- Whistles that appear across multiple channels
  - ○ A whistle may appear differently across channels. This can be caused when a
    dolphin produces the whistle while swimming and/or due to the loudness of
    the whistle. The hydrophone that is closest to the animal picks up the sound
    better than the other hydrophones. So the same whistle may appear across
    multiple channels and may look different on each channel. When this
    happens, you should imagine what the whistle would look like if all of its
    parts were combined and rate the whistle according to this imagined,
    combined whistle. However, you cannot add parts to your imagined whistle

that are not actually visible on any of the channels. In other words, use only

what you actually see.

APPENDIX E – IACUC Approval Letter

The University of
Southern Mississippi

*Institutional Animal Care
and Use Committee*

118 College Drive #5147
Hattiesburg, MS 39406-0001
Tel: 601.266.6820
Fax: 601.266.5509
www.usm.edu/spa/policies/animals

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

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

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

PROTOCOL NUMBER: **12080602**
PROJECT TITLE: **Enrichment and behavior observations in dolphins in the wild and in human care**
PROPOSED PROJECT DATES: **08/01/2012-07/31/2015**
PROJECT TYPE: **New**
PRINCIPAL INVESTIGATOR(S): **Heidi Lyn**
DEPARTMENT: **Psychology**
FUNDING AGENCY/SPONSOR:
IACUC COMMITTEE ACTION:
PROTOCOL EXPIRATON DATE: **7/31/2015**

_____
Jodie M. Jawor, Ph.D.
IACUC Chair

6 August 2012
Date

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