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Identifying the Social Contexts Present for Mouthing Behaviors in Bottlenose Dolphins (*Tursiops truncatus*)

by

Erin E. Frick

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

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ABSTRACT

Much of the research on dolphin communication has focused on the acoustic signals produced in a variety of social contexts. Although acoustic signals are undoubtedly an important aspect of dolphin communication systems, dolphin communication is multifaceted and multimodal (e.g., postural, visual and tactile signals, acoustic cues). The present study examined behaviors that involve the mouth (i.e., mouthing behaviors) in a group of captive dolphins using 2,696 minutes of underwater acoustic and video recordings collected from 2010 – 2014. Target behaviors are described as primarily visual (e.g., open-mouth display), both visual and acoustic (e.g., jaw claps), and tactile (e.g., mouthing, biting). Coding and analyses of the immediate behavioral antecedents and consequences (± 3 sec) surrounding each mouthing behavioral event revealed four context groups for mouthing behaviors using Latent Class Analyses: agonistic, affiliative, play, and sexual. Each mouthing event was assigned to a context group based on the strength of its probability of belonging to a given class. Overall frequencies of each focal mouthing behavior type and frequency of exhibiting a mouthing behavior in each context were highest for sub-adults and males for this population. These results present the first initial empirical evidence for social contexts other than aggression being present for mouthing behaviors in bottlenose dolphins.

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This project would not have been possible without the support of the Roatan Institute for Marine Sciences; I cannot thank the staff enough for their continued support of my research, including Teri and Eldon Bolton, and all the animal trainers at the RIMS facility.

Thank you to all my colleagues from the Marine Mammal Behavior and Cognition Lab for your input, assistance, and support. I would not have made it through this process without this wonderful group of researchers.

Finally, I would like to thank and honor my mentor, Dr. Stan Kuczaj, who passed away before this project was completed. The study of dolphin mouthing behavior was one of your passions before your passing, and I am honored and humbled to have been able to see this work through to its completion. I will be forever grateful for your unyielding support of this work and of my abilities as a researcher. I hope my continued research in this field will carry on part of your legacy, along with all of us impacted by our time spent working with you.

DEDICATION

I would like to thank my family, friends, and my StageStruck community for their steadfast and constant support during this process. It has been a long journey, and I am excited for the next chapter to begin in my professional career.

I’d like to dedicate this work to all women pursuing higher education in the sciences. No matter what difficulties, struggles, or hardships that may come your way, stay true to yourself and your goals; you can conquer anything.

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LIST OF ABBREVIATIONS

RIMS	Roatan Institute for Marine Sciences
MMBCL	Marine Mammal Behavior and Cognition Lab

CHAPTER I - INTRODUCTION

Behaviors exhibited by nonhuman animals are suggested to communicate information to other conspecifics, both deliberately and inadvertently (e.g., Paulos, Dudzinski, & Kuczaj, 2008). In particular, nonverbal behaviors related to the mouth are thought to serve a communicative role in a variety of species such as capuchin monkeys (*Cebus paella*; De Marco & Visalberghi, 2007), chimpanzees (*Pan troglodytes*; Waller & Dunbar, 2005; Van Hooff, 1973), white handed gibbons (*Hylobates lar*; Cooke & Schillaci, 2007), siamangs (*Symphalangus syndactylus*; Liebal, Pika, & Tomasello, 2004), bonobos (*Pan paniscus*; de Waal, 1988), collared lizards (*Crotaphytus collaris*; Lappin, Brandt, Husak, Macedonia, & Kemp, 2006), desert tortoise (*Gopherus agassizii*; Berry, 1986), spotted dolphins (*Stella frontalis*; Herzing, 1996), and bottlenose dolphins (*Tursiops truncatus*; Dudzinski, 1998; Herzing, 1996; Myers & Overstrom, 1978; Overstrom, 1983; Samuels & Gifford, 1997). In group-living species like cetaceans and primates, mouthing behaviors function across a wide range of contexts, such as agonistic (e.g., Myers & Overstrom, 1978; Overstrom, 1983; Parr, Waller, & Fugate, 2005), affiliation (e.g., Waller & Dunbar, 2005), courtship (e.g., Chivers, 1976), and grooming (e.g., Fox, 1977).

Group-living requires effective multimodal communication (i.e., vocalizations, nonverbal behaviors, postures, and signals; Parten & Marler, 1999) about environmental and internal states (Parr et al., 2005). Acoustic communication in animals is often based on our understanding of the nonverbal behaviors and responses associated with a particular vocalization (Herzing, 1996, 2000; Norris et al., 1994). However, a problem that continuously plagues scholars is the difficulty in agreeing upon operational definitions regarding the function of nonhuman nonverbal behaviors (Marler, Evans, & Hauser, 1992). For group-living species, the function of a particular behavior can be derived from the context in which it is performed (Prueschoft, 2000). Behavioral contexts do not refer to specific occurrences of behavioral events, but rather indicate general situational factors/states affecting a focal individual or group (de Waal, 2003; Frick, de Vere, & Kuczaj, 2017; Herzing, 1996; Paulos et al., 2008; Sebeok, 1965; Tavolga, 1983). Several scholars emphasize the need for analyses of contextual data in animal communication systems to examine concomitant behavior (i.e., all behaviors immediately preceding and following a focal event) rather than individual behaviors (de Waal, 2003; Herman & Tavolga, 1980; Herzing, 1996; Sebeok, 1965; Tavolga, 1983; Waller & Dunbar, 2005; Van Hooff, 1967). The use of a concomitant behavioral analytical strategy is observed in the study of mouthing behaviors in several studies of primates (e.g., de Waal, 2003; Liebal et al., 2004; Prueschoft, 2000; Waller & Dunbar, 2005; Van Hooff, 1967).

Investigations of multiple variations of open mouth threat displays in primates (i.e., mouth-open full – mouth is open fully with canine teeth visible; mouth-open half – mouth is partially open in an oval shape with canine teeth almost covered by the lips (Chivers, 1976; DeMarco & Visalberghi, 2007; Fox, 1977; Preuschoft, 2000; Preuschoft & Van Hooff, 1995, 1997)) suggests they may communicate different information dependent on the context (Van Hooff, 1973, 1995, 1997). For example, analysis of concomitant behaviors during post-display exchanges between actors and recipients supported the notion that silent bared teeth displays in chimpanzees are not limited to aggressive/agonistic contexts, but can signal different information across a variety of social and affiliative contexts (Waller & Dunbar, 2005). Relaxed open mouth displays in chimpanzees are correlated to both combat displays (Andrew, 1963) and play behaviors (Waller & Dunbar, 2005), possibly indicative of "play fighting" which utilizes behavioral patterns derived from aggressive fighting where the animals are able to distinguish the intent behind play and non-play signals (Pellis & Pellis, 1996, 1997). In tufted capuchins (*Cebus apella*), silent bared teeth displays are reported in both affiliative and submissive contexts (DeMarco & Visaberghi, 2007; Visalberghi et al., 2006); whereas white-tufted capuchins (*Cebus capucinus*) exhibit silent bared teeth more frequently in playful and affiliative contexts compared to agonistic or submissive contexts (Perry & Manson, 2004). Silent bared teeth displays are observed in a submissive context for macaque species with a strict dominance style (i.e., alpha male systems; *Macaca mulatta, M. fuscata, M. fascicularis, M. sylvabus*), and affiliative or social contexts in macaques with relaxed dominance styles (i.e., multi-male systems; *M. tonkeana, M. maura, M. nigra*) (De Marco et al., 2008; DeMarco & Visalberghi, 2007; de Waal & Luttrell, 1985; Preuschoft, 1995, 2004; Thierry, Iwaniuk, & Pellis, 2000).

Moreover, the communicative function of mouthing behaviors and facial displays in primates may change as an animal develops from infancy to adulthood (Chevalier-Skolnikoff, 1973). In chimpanzees, displays associated with socio-positive contexts typically appear earlier than those correlated to fear and aggression (Redican, 1975). The ontogeny of facial displays in a population of tufted capuchins was documented; where lip smacking appearing several weeks after birth, followed by scalp lifting, relaxed open mouth, silent bared teeth, open-mouth silent bared teeth, and open-mouth threat face appearing last during adolescence (De Marco & Visalberghi, 2007). This same population was also more likely to exchange these behaviors with individuals within their age-class, suggesting that age may serve a role in the types of displays exhibited and meaning behind those signals (De Marco & Visalberghi, 2007; De Marco et al., 2008).

Determining the context of a particular visual or acoustic signal via analysis of concomitant behavior (e.g., as observed in the primate literature) may also provide more accurate and quantitative measures in cetacean species. However, in-depth analysis of behavioral context in cetaceans has not been explored at length (e.g., Herzing, 1996; 2000; Würsig, Kieckhefer, & Jefferson, 1990) and has often been limited to surface observations due to the minimal ability to record cetacean behavior underwater (e.g., Dudzinski, 1998; Dudzinski, Clark, & Würsig, 1995; Herzing, 1996, 2000; Würsig et al., 1990). Only recently has technology allowed for simultaneous underwater video and acoustic data collection (i.e., Dudzinski et al., 1995). Systematic underwater data collection has facilitated identification of individuals performing and receiving a given behavior and has allowed for increased study of intraspecific signal exchange (i.e., communication) in cetaceans in captivity and the wild.

Paulos et al. (2008) utilized underwater data to investigate the communicative function of nonvocal behaviors of Atlantic spotted dolphins (*Stenella frontalis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in response to three operationally defined behavioral events: depart (one or more dolphins leaves the group), join (two or more dolphins come together), and contact (dolphins physically make contact with a part of the body). Each of the events coded was associated with a broad context group that described the overall activity of the dolphins at the time (i.e., general, social, foraging, play, travel, and inquisitive; see Dudzinski 1996, 1998). Touch behaviors were significantly associated with both depart and join events for both species. However, spotted dolphins were more likely to use touch after join events than before depart events, whereas Indo-Pacific bottlenose dolphins were equally likely to use touch with both event types.

Thus, tactile behaviors may communicate different information depending upon the context. Comparisons of pectoral fin contact behaviors between several populations of dolphins both wild and captive demonstrated that certain aspects of this contact behavior might be common to many dolphin species, whereas other components could be species-specific (e.g., Dudzinski, Danaher-Garcia, & Gregg, 2013; Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Dudzinski, Gregg, Ribic, & Kuczaj, 2009). Additionally, species-specific variation of pectoral fin contact could be the result of differing environmental and social conditions. Touch may not have an isolated, specific communicative function such as a greeting behavior, but may function more in establishing and maintaining social bonds throughout a given population (Caldwell & Caldwell, 1977; Connor, Smolker, & Richards, 1992; Dudzinski, 1998; Herzing, 1996; Paulos et al., 2008; Pryor, 1990; Sakai, Hishii, Takeda, & Kohshima, 2006).

Tactile behaviors in bottlenose dolphins are not limited to pectoral fin interactions, but can also involve the mouth (Tavolga, 1983). There are four types of mouthing behaviors frequently observed in dolphins: jaw clap threats, bite, open mouth displays and mouthing. Jaw claps are defined as a dolphin opening and closing its jaws in a sharp, rapid manner (Caldwell & Caldwell 1967; Dudzinski, 1996, 1998; Herzing, 2000; Holobinko & Waring, 2010; McCowan & Reiss, 1995; Overstrom, 1983; Samuels & Gifford, 1997). It is a nonvocal behavior, but is considered an acoustic signal due to the “pop” sound created, which exhibits measurable variables (i.e., frequency, rate, spacing; Herzing, 2000). Bites are defined as abrupt and forceful contact with another dolphin, using teeth, which may result in rake marks appearing on the recipient (Caldwell & Caldwell, 1967; Defran & Pryor, 1980; Dudzinski, 1996, 1998; Essapian, 1953, 1962, 1963; Herzing, 1996, 2000; Johnson & Norris, 1986; Lawrence & Schevill, 1954; McBride, 1940; McBride & Hebb, 1948; Norris, 1967, Ostman 1991; Overstrom 1983; Perazio & Kuczaj, 2017; Pryor, 1973; Pryor & Kang, 1980; Saayman, Tayler, & Bower, 1973; Samuels & Gifford, 1997; Tavolga, 1966, Tavolga & Essapian, 1957; Tayler & Saayman, 1972). Across animal taxa, a bite is understood to be a highly aggressive behavior (e.g., Collias, 1944; Blanchard, Fukunaga, Blanchard, & Kelley, 1975; Deckel, 1995; McGlone, 1985; Samuels & Gifford, 1997; Washburn & Hamburg, 1968; Wright, 1991). In dolphins, bite and jaw clap threats are considered agonistic/aggressive signals, observed in adult dolphin exchanges involving other agonistic behaviors such as hits, rams, chases, body slams, and pins (Kuczaj & Frick, 2015; Myers & Overstrom, 1976; Overstrom, 1983; Samuels & Gifford, 1997; Veit & Bojanowski 1996).

Open mouth displays are defined as one dolphin's mouth opened and directed at another dolphin, which can be accompanied by vertical head movements and rotation of the body (Bateson, 1974, Caldwell & Caldwell, 1967, Caldwell et al., 1998; Defran & Pryor, 1980; Dudzinski, 1996, 1998; Essapian, 1953, 1962, 1963; Herzing, 1996, 2000; Johnson & Norris, 1986; Lawrence & Schevill, 1954; McBride, 1940; McBride & Hebb, 1948; Norris, 1967, Ostman 1991; Overstrom 1983; Perazio & Kuczaj, 2017; Pryor, 1973; Pryor & Kang, 1980; Saayman et al., 1973; Samuels & Gifford, 1997; Tavolga, 1966, Tavolga & Essapian, 1957; Tayler & Saayman, 1972; Wood, 1953; Würsig et al., 1990). Mouthing involves a dolphin open its mouth around the body of another (typically the peduncle/caudal region) with no apparent attempt to bite down on the recipient (Cockcroft, 1989; Kuczaj & Yeater, 2007; Lockyer & Morris, 1985; Saayman et al., 1973; Shane, Wells, & Würsig, 1986). The ontogeny of open mouth and mouthing behaviors in dolphin calves begins with the acquisition of teeth (160 days), which is associated with the first observance of mouthing (Cockcroft, 1989). Additionally, infant dolphins experience a developmental shift in the production of pulsed sounds, where the mouth is open to a closed mouth (Reiss, 1998). The anatomical basis for this shift is unknown at this time. Other developmental markers include play herding in dolphin calves where males display an open mouth at one another, first observed within 6 – 12 months of life (Gibson & Mann, 2008; Tavolga, 1983). Dolphin calves also use open mouth chases to corner fish near the surface, a developmental precursor to adult foraging (Amundin, 1986; Caldwell & Caldwell, 1972, Cockcroft & Ross, 1990; Essapian, 1953; Gibson & Mann, 2008).

Open mouth displays in dolphins are predominantly categorized in the literature as threat displays. Caldwell and Caldwell (1967) investigated chase-open mouth attacks – where one dolphin exhibits an open mouth while chasing another dolphin mouthing the caudal region of the fleeing dolphin with no attempt to bite – and reported that open mouth displays served an agonistic function, advertising 'threat.' Myers and Overstrom (1978) similarly described two captive dolphins from adjacent holding areas rapidly approach one another head on until reaching the net barrier that divided the pool. The pair would exhibit rapid head movements, burst pulse vocalizations, simultaneous bubble bursts, open mouth displays where the jaws could touch through the barrier, and jaw claps until the interaction terminated after several seconds (i.e., one of the dolphins swam away). The behaviors comprising these interactions were classified as aggressive (DeFran & Pryor, 1980; Myers & Overstrom, 1976). Subsequent observations by Overstrom (1983) of the same population included similar head to head open mouth interactions (Myers & Overstrom, 1976) as well as chase-open mouth attacks (Caldwell & Caldwell, 1977). These open mouth exchanges were frequently accompanied by tail-slapping, chasing, and violent contact with one another, which suggests that these open mouth displays were aggressive (Overstrom, 1983). Additionally, submissive posturing such as flank area presentation (Caldwell & Caldwell, 1977) was frequently displayed by the dolphin being chased. Jaw claps were used as an index of aggression in these interactions as they occurred three times more frequently when open mouth displays and burst pulse vocalizations were exhibited and reciprocated by another dolphin (Overstrom, 1983). This often preceded an escalation of aggressive contact. Overstrom (1983) also described mouthing as a form of threat, as its occurrence similarly preceded an intensification of aggressive contact. However, it is important to note that there were several instances of non-aggressive open mouth displays and mouthing, characterized by the dolphins synchronously swimming 'peacefully' around the enclosure with no specific behavioral events indicated (Overstrom, 1983). This suggests additional communicative functions beyond aggression may be present for these mouthing behaviors.

Open mouth displays, mouthing, jaw claps, bite are also observed in discipline exchanges between mothers and calves. Discipline in cetaceans involves the mother (or alloparent) punishing another individual to extinguish undesirable behavior (Hill, 2009; McCowan & Reiss, 1995; Weinpress & Herzing, 2015) and/or to reestablish order (Herzing, 1996). Weinpress and Herzing (2015) investigated discipline behaviors and interactions in Atlantic spotted dolphins and found that display behaviors (such as open mouth and jaw clap) were not observed as frequently as pursuit behaviors (i.e., chase). Display behaviors did not require proximity or physical contact, and were 25% less likely to successfully reduce/extinguish undesirable behaviors from the calf. Contact behaviors (i.e., bite) were observed less frequently than display and pursuit behaviors. Aggressive contact behaviors such as pin and bite are considered highly effective disciplinary action, albeit dangerous and risky due to the potential for serious injury and even death to a young calf or juvenile (Connor et al., 1992; Cusick & Herzing, 2014; Dunn, Barco, Pabst, & McLellan, 2002; Herzing & Johnson, 1997; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2004).

Furthermore, mouthing behaviors are reported as a response to both familiar and novel stimuli, such as a reflective surface (e.g., mirror). Reiss and Marino (2001) examined mirror self-recognition (MSR) in dolphins and reported a subject that was marked on his tongue, swimming up to the mirror opening and closing its mouth repeatedly. Delfour (2006) observed dolphins engaging in open mouth displays for a long duration (greater than 5s) when allowed to interact with a mirror. Delfour and Herzing (2013), Lopes et al. (2016), and Sarko et al. (2002) included open mouth displays and jaw claps as behaviors indicative of an aggressive response to a mirror/reflective stimuli. The individual frequency of these open mouth displays and jaw claps is unknown, as in each study they were grouped with other aggressive behaviors (i.e., tail slap, vertical head shake, etc.). Additionally, Lopes et al. (2016) reported that when dolphins of varying age-class and sex were presented with novel stimuli (e.g., a reflective surface and a non-reflective surface), both adults and calves engaged in more aggressive interaction with the reflective surface vs. the non-reflective surface. However, when Marten and Psarakos (1995) presented dolphins with (1) live feed of themselves at the mirror and (2) playback video of earlier behaviors via a television, the dolphins engaged in more open mouth behaviors and presentation of marked body parts during the mirror condition, suggesting that mouthing behaviors in this context were self-examination. Morrison (2014) similarly observed frequent open and closing of the mouth when the dolphins were presented with a mirror, suggesting a possible exploratory context for mouthing behaviors.

Open mouth displays and mouthing are also both present in exploratory play with novel objects, as well as social play with other conspecifics (Kuczaj & Eskelinen, 2014; Kuczaj & Makecha, 2008). A variety of objects have been successfully used as enrichment for cetaceans (Eskelinen et al., 2015; Kuczaj et al., 2002; Kuczaj et al, 2006; Kuczaj & Highfill, 2005; Kuczaj & Yeater, 2007; Lopes et al., 2016; Paulos et al., 2010). Interaction with objects can be indicative of object play (Bekoff & Byers, 1998, Weaver & Kuczaj, 2016). The objects for enrichment or object play include both man-made (i.e., ball, buoys) and naturally occurring (i.e., seaweed, sticks, leaves, grass; Eskelinen et al., 2015; Greene, Melillo-Sweeting, & Dudzinski, 2011; Kuczaj et al., 2006; Weaver & Kuczaj, 2016). Most reports of play in cetaceans state that toys are typically carried in the mouth (i.e., mouthing) or other body parts, and/or passed around the body or between other members of the social group (Kuczaj et al., 2006; Paulos et al., 2010; Weaver & Kuczaj, 2016). Bubble play behaviors (i.e., single bubble, bubble trail, single bubble ring, and double bubble ring) can involve mouthing and open mouth displays in response to the bubble, or to further manipulate the bubble as a form of play (Jones & Kuczaj, 2014; McCowan, Marino, Vance, Walke, & Reiss, 2000; Moreno, 2017). Additionally, Winship and Eskelinen (*submitted*) analyzed responses of bottlenose dolphins and rough-toothed dolphins (*Steno bredanensis*) to novel video clips as a form of enrichment. Overall, male bottlenose dolphins exhibited high frequencies of aggressive responses (e.g., including open mouth displays and jaw claps) toward the television (Winship & Eskelinen, submitted). Marten and Psarakos (1995) similarly noted two male bottlenose dolphins engaging in open mouth display and head jerk behaviors (i.e., aggression) when presented with a television. However, Hanna and colleagues (2017) suggest that the open mouth displays observed by a killer whale's (*Orcinus orca*) response to video media indicated its interest. These results across studies suggest that the interpretation of open mouth displays during video enrichment may be dependent on context and individual preferences of the animal.

As demonstrated through the prior discussion of the literature currently available on mouthing behaviors in bottlenose dolphins, it is commonly reported that they serve as aggressive signals. However, there have been several reports of mouthing behaviors in various cetacean species occurring in different contexts. When analyzing psychophysical responses to uncertainty using an auditory discrimination task in a bottlenose dolphin, Smith et al. (1995) found that as the task increased in difficulty, the dolphin engaged in rhythmic opening and closing of the mouth accompanied by side-to-side head movements. Open mouth displays and mouthing were components of multiple socio-sexual exchanges in young male bottlenose dolphins (Lockyer & Morris, 1985; Mann, 2006; Saayman et al., 1973; Shane et al., 1986) and belugas (*Delphinapterus leucas*; Hill et al., 2015). In response to an object transformation task, bottlenose dolphins exhibited bubble bursts and open mouth displays that were concluded to be non-aggressive and more indicative of surprise/excitement or interest (Lilley, de Vere, & Yeater, 2018). Rough toothed dolphins engaged in mouthing as a form of affiliative contact (Kuczaj & Yeater, 2007). Thus, it is likely that mouthing behaviors in dolphins may serve a communicative role in contexts other than aggression.

Kuczaj and Frick (2015) presented results from pilot data analyzing the concomitant behavior surrounding dolphin-dolphin mouthing exchanges (i.e., open mouth displays, mouthing, bite, and jaw clap), which suggested these behaviors occur in at least three contexts: affiliative, sexual, and confrontational/agonistic. Only open mouth displays and mouthing were observed across the three contexts, whereas biting and jaw claps were exclusively exhibited in the confrontational context. Preliminary results on age and sex differences suggested that overall, males engage more frequently in mouthing behaviors compared to females. For both sexes, the individuals that produced the most open mouth and mouthing events were younger animals located in the middle of the social hierarchy, suggesting that such signals may be especially important for animals attempting to either increase or establish their social status.

Current Study

The aim of the present study sought to empirically determine the function of behaviors related to the mouth across social contexts for a group of bottlenose dolphins housed at the Roatan Institute for Marine Science (RIMS) using underwater video data from 2010-2014. Target behaviors included open mouth displays, jaw claps, mouthing, and biting; hereafter referred to collectively as mouthing behaviors/events, in varying social contexts. Each mouthing behavior/event was coded (±3s) to examine the antecedent and consequent affiliated with each focal event (i.e., analysis of all concomitant behavior as observed in studies of primate mouth-open displays (e.g., Van Hooff, 1972, 1973, Waller & Dunbar, 2005)). Demographic information (e.g., age-class, sex, social rank) was collected and analyzed to assess individual variations that may be present in mouthing behavior usage across the emergent social contexts.

The current study utilized the pilot data from Kuczaj and Frick (2015), as well as supplemental data recordings from 2012 – 2014. It was predicted that the inclusion of additional data would reveal new contexts in dolphin-dolphin exchanges not found in the pilot data, such as a play context. It was hypothesized that all open mouth displays and mouthing would be exhibited across multiple contexts, and that the contexts would vary across each behavior type. Jaw claps and bites were hypothesized to occur only in confrontational/aggressive contexts as seen in the pilot data. It was predicted that individual differences would present in the type of mouthing behavior exhibited and context based on age class and sex of the animal.

CHAPTER II - METHODS

Subjects and Facility

The dolphin population used for this study is housed at the Roatan Institute for Marine Sciences (RIMS hereafter) located on Roatan island on the north-west side of the Honduran coast. The dolphins reside in an enclosed sea pen approximately 8,000m^2, with a depth range from the shoreline to approximately 7m (Figure 1). The population consisted of both males and females (N = 24 – 30) of varying age classes (i.e., calf – dependent and nursing, sub-adults –independent but not sexually mature, and adults – independent and sexually mature; Eskelinen et al., 2015); with eight calves born during the duration of the study (2010 – 2014; see Table 1). The facility manager, Teri Bolton, provided all data pertaining to the sex and age-class of the dolphins.

Figure 1. Ariel photograph of Roatan Institute for Marine Science dolphin enclosure.

Table 1

Demographic Information for RIMS Dolphins

Name	Sex	Birth Date	Age Class
Mac	M	08/05/13	Calf
Lenca	M	07/27/12	Calf
Champion	M	07/05/12	Calf
Elli	F	07/31/12	Calf
Calli	F	07/28/12	Calf
Polly	F	07/25/11	Calf
Tilly	F	08/14/11	Calf
Cortez	M	05/02/10	Calf
Mickey	M	07/11/09	Sub-Adult
Vin	M	08/04/09	Sub-Adult
Dixon	M	09/04/07	Sub-Adult
Anthony	M	10/01/05	Sub-Adult
Mr. French	M	08/13/04	Sub-Adult
Ken	M	09/30/04	Sub-Adult
Ritchie	M	10/30/03	Sub-Adult
Pigeon	F	08/13/09	Sub-Adult
Bailey	F	10/13/05	Sub-Adult
Margarita	F	08/14/07	Sub-Adult
Fiona	F	10/25/03	Sub-Adult
Ronnie	M	11/10/02	Adult
Bill	M	12/16/01	Adult
Han Solo	M	05/02/09 *	Adult
Hector	M	07/06/03 *	Adult
Paya	M	10/30/89 *	Adult
Maury	F	01/14/02	Adult
Mika	F	08/20/01	Adult
Alita	F	07/06/03 *	Adult
Carmella	F	10/30/03 *	Adult
Gracie	F	09/29/98 *	Adult
Cedena	F	10/03/90 *	Adult
Mrs. Beasley	F	12/04/98 *	Adult

* = Wild born, acquisition date.

Data Collection

Dr. Stan Kuczaj and graduate students from the Marine Mammal Behavior and Cognition lab (University of Southern Mississippi) collected underwater video and audio data using a Nauticam M16 with Amphibico hydrophone adapter, which allowed for simultaneous audio and video data. Underwater videos were recorded opportunistically, during yearly excursions to RIMS facility in Roatan, Honduras from 2010 – 2014, totaling 2,696 minutes of data. The data was collected using focal-animal, focal-sub group, and all-occurrence sampling (Altmann, 1974). Focal follows began when an animal came into view and terminated when the animal disappeared from view (Dudzinski et al., 2009). Video segments ranged from several seconds to approximately 10 minutes. Data were collected opportunistically between the hours of 6:00am – 4:00pm (n = 3,768) during off session (free swimming) conditions. All videos during training sessions or dolphin dive excursions were excluded from analysis.

Data Coding

All videos were analyzed to identify all events of the four target behaviors: open mouth displays, mouthing, bite, and jaw clap (for operational definitions, see Appendix A). A comprehensive ethogram consisting of 35 dolphin behaviors were recorded 3 seconds prior, during, and 3 seconds following each event (i.e., before, during, and after). All occurrences of target mouthing behaviors (Appendix A) exhibited by the focal animal (as the actor or recipient) were recorded in respect to the three time periods. All subjects were identified via permanent features through the use of photographs (i.e., dorsal fins, flukes, pectoral fins, dorsal and ventral views).

For each target behavior, the duration for an event began at the onset of the dolphin opening its mouth, and concluded when the dolphin’s mouth was completely closed, or if the focal dolphin was out of screen for more than six frames of video. The duration of that target behavior was recorded, with ±3 seconds added to account for the before and after time periods respectively. Each time period (i.e., before, during, and after) was coded for all concomitant behaviors (Appendix A) from the perspective of the mouthing (focal) dolphin (i.e., only behaviors exhibited by and toward the focal dolphin). If the focal dolphin exhibited another target behavior within the ±3 seconds, that occurrence of a target behavior was coded in the appropriate before or after time period. Additionally, each of the target mouthing events was coded as its own separate focal event, all while maintaining a record of the sequential interactions and exchanges where multiple mouthing behaviors were observed. This was done to account for an escalation in mouthing behaviors as noted previously in bottlenose dolphins (e.g., Myers & Overstrom, 1978; Overstrom, 1983). Each focal event was also coded for what or whom the mouthing behavior is directed toward – another dolphin within the same group, dolphin in a different group, object, person, or unknown (see Appendix A). Only dolphin-dolphin social exchanges were utilized for analyses.

Fifteen researchers from the Marine Mammal Behavior and Cognition Laboratory (University of Southern Mississippi) participated in the data coding for this project. Inter-coder reliability across all individuals was assessed using Pearson Correlation Coefficient for all behaviors coded in the three time periods (before, during, and after), mouthing behavior (open mouth displays, mouthing, bite, and jaw clap), and the identity of all mouthing dolphins and recipients. Reliability was achieved at 80% agreement or higher between all researchers.

Statistical Analyses

Classification of context for all mouthing events was assessed using a Latent Class Analysis (LCA). The use of LCA is shown to be an effective tool to observe relationships between dichotomous variables (Goodman, 2002). This analysis allows for the analysis of manifest relationships of effects present across numerous variables (Marsh et al., 2009). Each class, like a cluster, will group together homogeneous cases (i.e., concomitant behaviors that occur together predictably). Comparisons of cluster and factor analyses to LCA demonstrate that statistically LCA outperforms and provides an improved model fit, typically resultant in 3-5 classes (Magidson & Vermunt, 2001). The results of these LCA analyses provided the concomitant behaviors that clustered together significantly (e.g., hit, chase, bite) that collectively were categorized as a context group (e.g., agonistic) for which a focal mouthing event occurred (Kuczaj & Frick, 2015). Additionally, the LCA calculates the probability of each focal mouthing event belonging to each class that emerges from the analysis, and assigns each individual event to one context group based upon which class the event has the highest probability of belonging too.

During the termination of model, behaviors that were extremely infrequent compromised the model from (i.e., output generated a message that stated the model was untrustworthy) and subsequently were step-wise eliminated from the model until the model output terminated normally. Behaviors that fell within these criteria were any behavior whose frequency was less than 10 within the before time period (e.g., abrupt horizontal head movement, hit recipient, herd/herd recipient, head scanning, orient to person, petting, orient to object, tactile recipient, jaw clap recipient, bite recipient); the during time period (e.g., avoid/flee, orient to object, petting, hit/hit recipient, pectoral fin rub recipient, orient to object, orient to person), and after time period (e.g., approach recipient, abrupt horizontal head movement, herd/herd recipient, head scanning, orient to object, orient to object, petting). Similarly, behaviors whose frequencies were nearly constant similarly compromised the model, and were subsequently eliminated from the model in order for the model output to be trustworthy. This excluded the highly frequent behavior solo swim ($n > 4000$) from the model and future analyses.

During the optimization of the model, behaviors within a class that approached the logit thresholds were set at extreme values (i.e., Est. ±15.00, SE = 0, $p = 999.00$) within a class, and were excluded from further analysis for a given class. Multiple behaviors loaded significantly into multiple classes, but only behaviors with the highest probability of belonging to a given class compared to all others were considered when labeling each class (i.e., > 0.5). The highest probability was indicated by whether the behavior significantly loaded into the class (i.e., $p < 0.05$), and the calculated output probability scale of that behavior belonging to that class was the highest proportion value compared to all other classes (i.e., proportion between 0.00-0.99). This was confirmed by cross-checking the Estimate/Standard Error (Est./SE) values for each behavior across all classes, as the higher Est./SE value was also indicative of the highest probability scale for a given behavior for a given class.

Following all coded mouthing events being categorized with a context group, further analysis of individual differences related to use of mouthing events in certain contexts were conducted. Individual differences in overall frequency of each mouthing display type, per context, were compared using multinomial regression. Loglinear analyses determined which interactions between age, sex, mouthing type, and context were significant. The loglinear analysis was followed by chi-square test of independence for all interactions identified as significant. These allowed for comparisons of age-class and sex for the mouthing behavior type and context exhibited.

CHAPTER III - RESULTS

Latent Class Analysis

Using a latent class analysis, the best-fit model was identified at four classes (k = 4, $p < 0.05$) as indicated by the smallest values obtained for Akaike (AIC), Bayesian Information Criteria (BIC), and Sample Adjusted BIC and higher values for Entropy(E_k). Smaller values for AIC, BIC and Adjusted BIC indicate improved model fit and trustworthiness of the model. Entropy (E_k) measures how clearly distinguishable the classes are based on how distinctly each individual's estimated class probability is, with values over 0.8 indicative of strong individual classification of each focal event (Table 2). Prevalence of each class occurring across the model was calculated (Table 3).

Table 2

Latent Class Analysis Model Fit

	3 CLASSES	**4 CLASSES**	**5 CLASSES**
AIC	88675.501	86257.863	87293.010
BIC	90288.871	88411.192	89986.298
SAMPLE ADJUSTED BIC	89500.814	87359.390	88670.751
ENTROPY	0.751	0.825	0.775
***N* FOR EACH CLASS**	C1: 2053 C2: 964 C3: 1925	C1: 1966 C2: 498 C3: 697 C4: 1781	C1: 427 C2: 382 C3: 934 C4: 1476 C5: 1723

The 4-class model was chosen based on higher entropy and lower BIC and AIC.

Table 3

Overall Class Prevalence for the Model

LATENT CLASS	PREVALENCE
C1: AFFILIATIVE	41%
C2: SOCIO-SEXUAL	10%
C3: PLAY	14%
C4: AGONISTIC	35%

All classes were labeled based on significant and high-probability behavioral response patterns for each latent grouping to identify the following context groups: affiliative (class 1), socio-sexual (class 2), play (class 3), and agonistic (class 4) (Table 4). Each individual event was assigned to a class (i.e., context group) based on the highest calculated probability by the model for an event to belong to a class (i.e., between 0-0.99). Each event's probability was 0.5 or higher in order for the event to be categorized as belonging to a given class.

Table 4

Behaviors Retained to Identify Each Context Group

Context Group	Key Identifying Behaviors
Affiliative	**Before:** bubble trail, hit, rub, tactile recipient, open mouth display, open mouth display recipient, mouthing recipient, pectoral fin rub recipient **During:** pair swim with contact, bubble burst, group social ball, orient different group, rub **After:** pair swim with contact, approach, avoid/flee, abrupt horizontal head movement, bubble trail
Sexual	**Before:** group swim, avoid/flee, orient to camera, pectoral fin rub, sexual contact, approach recipient, herd **During:** pectoral fin rub, sexual contact **After:** pair swim, hit recipient, orient to camera, orient to person, tactile recipient, bite, pectoral fin rub, rub, sexual contact
Play	**Before:** bubble burst, group social ball, tactile, mouthing **During:** abrupt vertical head movement, orient same group, orient to camera, tactile **After:** chase, group social ball, mouthing, pectoral fin rub recipient, tactile
Agonistic	**Before:** approach, approach recipient, chase, abrupt vertical head movement, hit recipient, orient different group, orient same group, rub recipient, bite, jaw clap **During:** pair swim, group swim, approach, chase, abrupt horizontal head movement, bubble trail, rub recipient, tactile recipient, open mouth recipient, mouthing recipient **After**: group swim, bubble burst, hit, rub recipient, open mouth, open mouth recipient, mouthing recipient, jaw clap

Behaviors utilized for labeling each class were derived by taking the behaviors that significantly clustered and had the highest probability of belonging to that class.

Within the LCA model, each focal mouthing event (*N* = 4,942) was assigned to each of the (4) classes based on the extent to which class the event had the strongest probability of belonging (i.e., the model calculated and assigned each event a proportion between 0.00-0.99, where the highest value indicates the highest likelihood of belonging) and then assigned the class number with the highest proportion to each individual event. All mouthing behaviors, open mouth display (*n* = 4,665), mouthing (*n* = 211), bite (*n* = 25), and jaw clap (*n* = 41), were exhibited across all four context groups (Figures 2-4). Bite and jaw claps were exhibited at extremely low frequencies, but were retained for analysis and discussion due to their established role as an index of aggression in bottlenose dolphins (e.g., Myers & Overstrom, 1978; Scott et al., 1995).

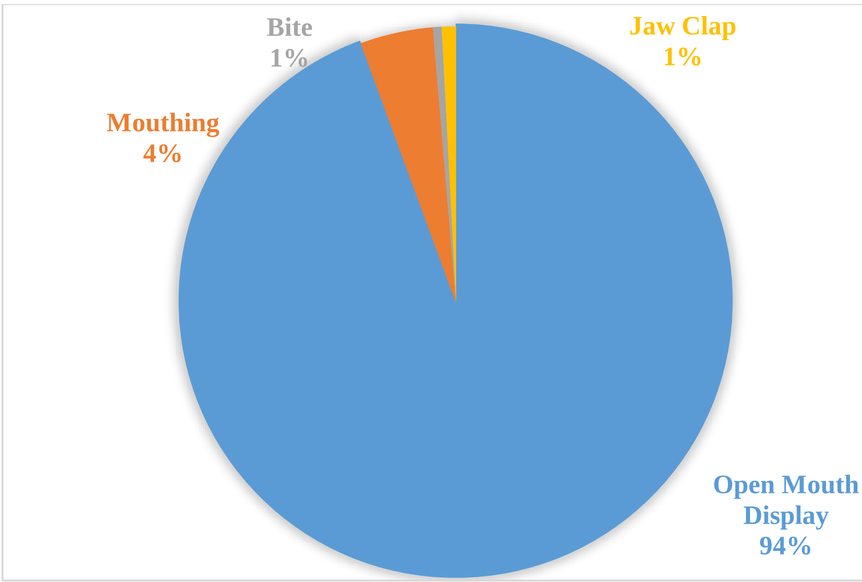

Figure 2. Percentage of mouthing events by type.

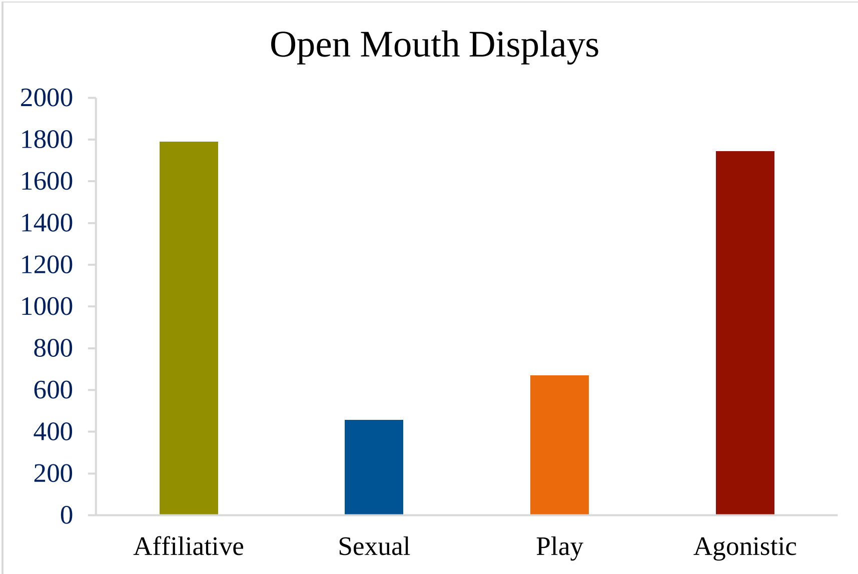

Figure 3. Frequency of open mouth displays across the four context groups.

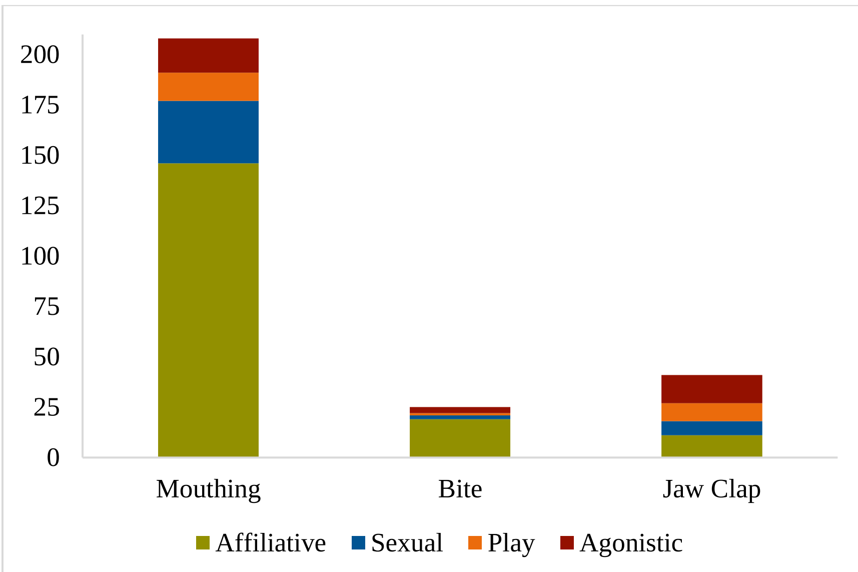

Figure 4. Frequency of mouthing, bite, and jaw clap across the four context groups.

Differences between whether a particular mouthing behavior was more or less likely to occur in a particular context was compared utilizing multinomial logistic regression analyses. Significant comparisons between which context group was more likely to occur for each mouthing type were present ($\chi^2(9) = 140.59$, $p < 0.01$). All comparisons were made to the affiliative context, due to it being the most frequently observed context group. Compared to the affiliative context, there was a 40% less likelihood of open mouth displays occurring in the sexual context (B = -0.91, SE = 0.49, Wald = 3.52, $p = 0.06$), 34% less likelihood of mouthing occurring in the sexual context (B = -1.07, SE = 0.52, Wald = 4.18, $p = 0.04$), 3) a 17% less likelihood of bite occurring in the sexual context (B = -1.78, SE = 0.89, Wald = 4.11, $p = 0.04$). Compared to the affiliative context group, there was a 46% less likelihood of open mouth displays occurring in the play context (B = -0.78, SE = 0.45, Wald = 2.97, $p = 0.08$), a 13% less likelihood of mouthing occurring in the play context (B = -2.08, SE = 0.53, Wald = 15.63, $p < 0.00$), and a 6% less likelihood of bite occurring in the play context (B = -2.74, SE = 1.12, Wald = 6.00, $p = 0.01$). Compared to the affiliative context, there was a 10% less likelihood of mouthing occurring in the agonistic context (B = -2.33, SE = 0.47, Wald = 24.25, $p < 0.00$), and a 12% less likelihood of bite occurring in the agonistic context (B = -2.09, SE = 0.74, Wald = 7.94, $p = 0.01$). Comparisons of open mouth displays between the affiliative and agonistic contexts were non-significant. Overall, jaw claps were unable to be compared across contexts due to their skewed distribution.

Age-Class Analyses

Loglinear analyses revealed that there was an overall main effect based on age-class, mouthing type, and behavioral context. K-way effects were non-significant for a 3-way interaction, indicating it should be removed ($\chi^2(18) = 13.29$, K = 3, $p = 0.91$). Interactions between two variables (mouthing type*age-class; behavioral context*age-class) were significant ($p < 0.01$) and identified for subsequent chi-square analyses between each 2-way interaction.

A Chi-square test of independence was calculated comparing the frequency of each mouthing type across age-class for all dolphin subjects (Figures 5 – 8). A significant interaction was found ($\chi^2(6, N = 4{,}516) = 13.58$, $p = 0.03$). Comparisons were made in reference to sub-adults, who exhibited each behavior type most frequently for all mouthing behaviors. Sub-adults open mouth displays (*n* = 2,262, Std. Residual = -0.30) accounted for 53% of all open mouth displays observed, compared to 23% adults (n = 970, Std. Residual = -0.10) and 24% in calves (*n* = 1,026, Std. Residual = 0.50). For all mouthing behavior, sub-adults exhibited the highest frequencies, accounting for 57% of the behaviors observed (*n* = 114, Std. Residual = 0.70), compared to 22% for adults (*n* = 44, Std. Residual = -0.2) and 21% for calves (*n* = 41, Std. Residual = -0.9). For all bite behaviors, 68% were exhibited by sub-adults (*n* = 15, Std. Residual = 0.9), compared to 22% for adults (*n* = 5, Std. Residual = 0.00) and calves (*n* = 2, Std. Residual = -1.40). Jaw claps were also most frequently observed by sub-adults (*n* = 21, Std. Residual = 0.30) accounting for 56% compared to the 38% of jaw claps observed by adults (*n* = 14, Std. Residual = 1.9) and 5% by calves (*n* = 2, Std. Residual = -2.30).

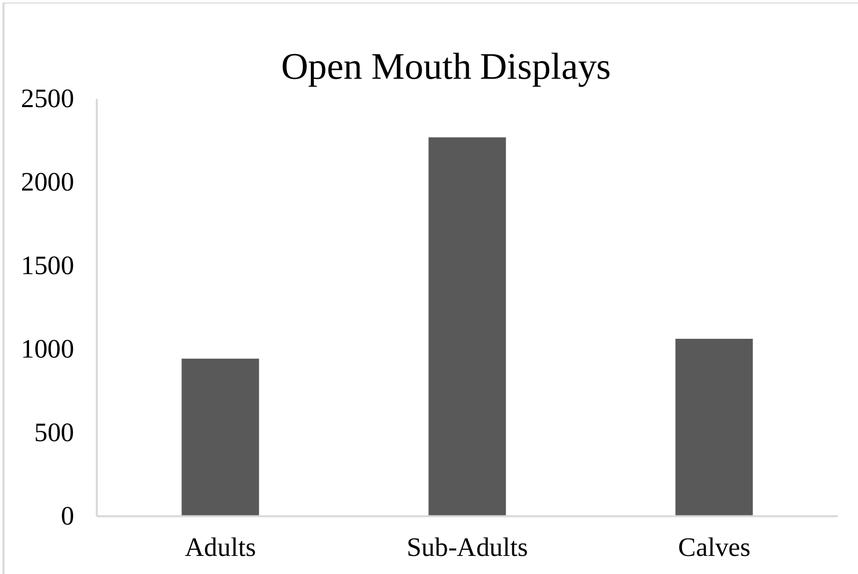

Figure 5. Frequency of open mouth displays by age-class.

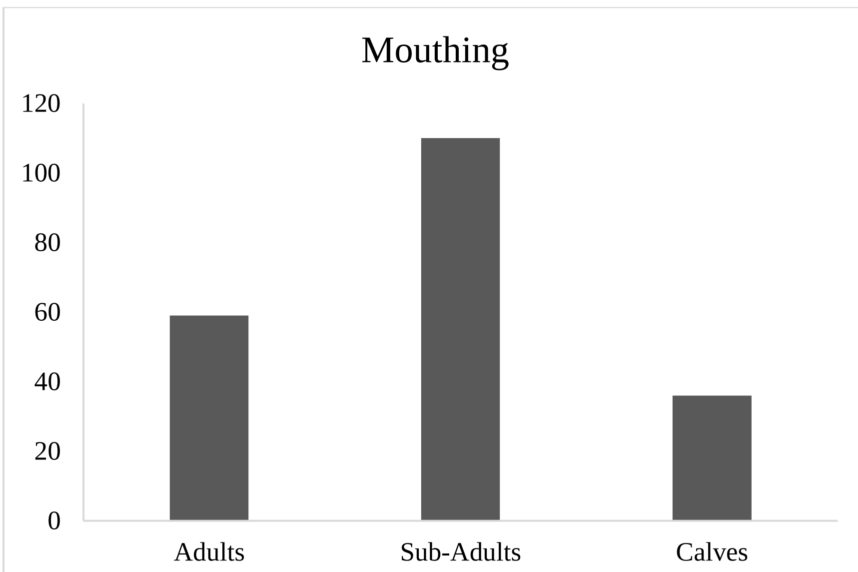

Figure 6. Frequency of mouthing behavior by age-class.

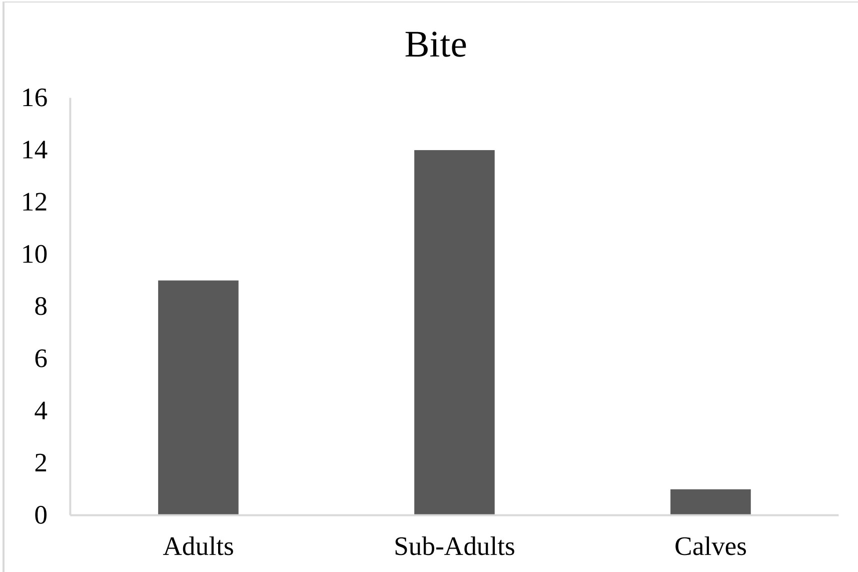

Figure 7. Frequency of bite behavior by age-class.

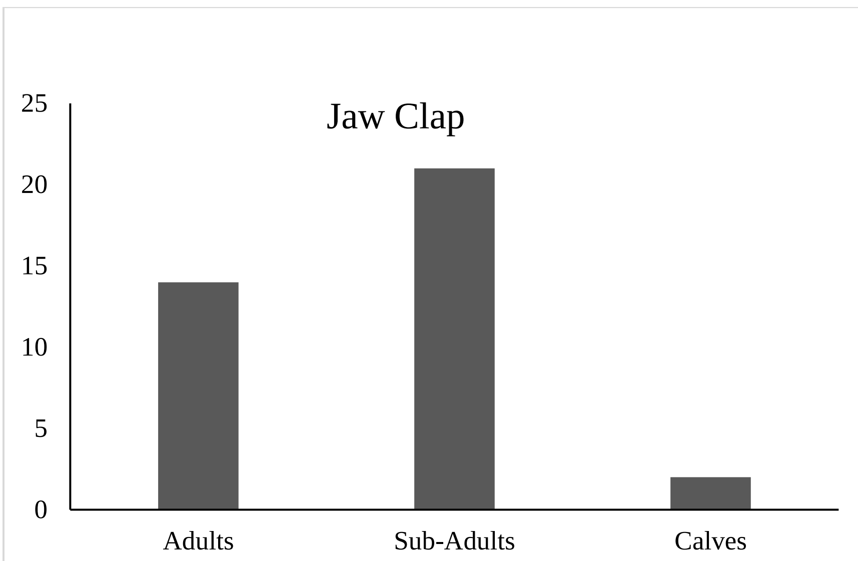

Figure 8. Frequency of jaw-clap behavior by age-class.

A Chi-square test of independence was calculated comparing the frequency of behaviors exhibited in each context across age-class for all dolphin subjects (Figures 9 – 12). A significant interaction was found ($\chi^2(6, N = 4{,}516) = 27.3, p < 0.00$). Comparisons were made in reference to sub-adults, who exhibited the highest frequencies of all behaviors in each context group. Sub-adults (n = 1,026, Std. Residual = 0.90) accounted for 55% of all affiliative mouthing behaviors observed, compared to 22% adults (*n* = 418, Std. Residual = -0.40) and 23% in calves (*n* = 423, Std. Residual = -0.90). For all sexual mouthing behaviors, sub-adults exhibited the highest frequencies, accounting for 57% of the behaviors observed (*n* = 264, Std. Residual = 1.10), compared to 17% for adults (*n* = 78, Std. Residual = -2.70) and 26% for calves (*n* = 120, Std. Residual = 1.00). For all play mouthing behaviors, 50% were exhibited by sub-adults (*n* = 312, Std. Residual = -1.10), compared to 26% for adults (*n* = 132, Std. Residual = -0.80) and calves (*n* = 177, Std. Residual = 2.40). Mouthing behaviors in the agonistic context group were also most frequently observed by sub-adults (*n* = 810, Std. Residual = -0.90) accounting for 52% compared to the 26% observed by adults (*n* = 405, Std. Residual = 2.50) and 22% by calves (*n* = 351, Std. Residual = -1.10).

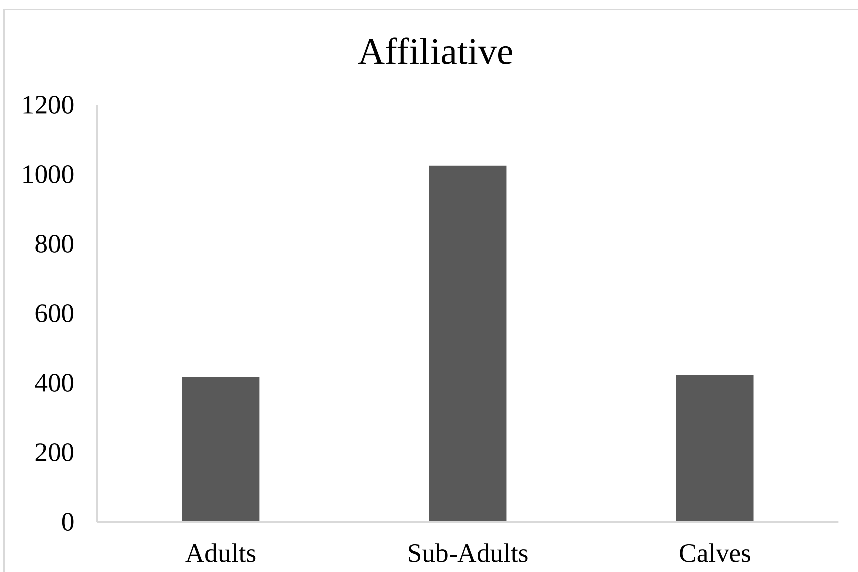

Figure 9. Frequency of overall mouthing behaviors in the affiliative context by age-class.

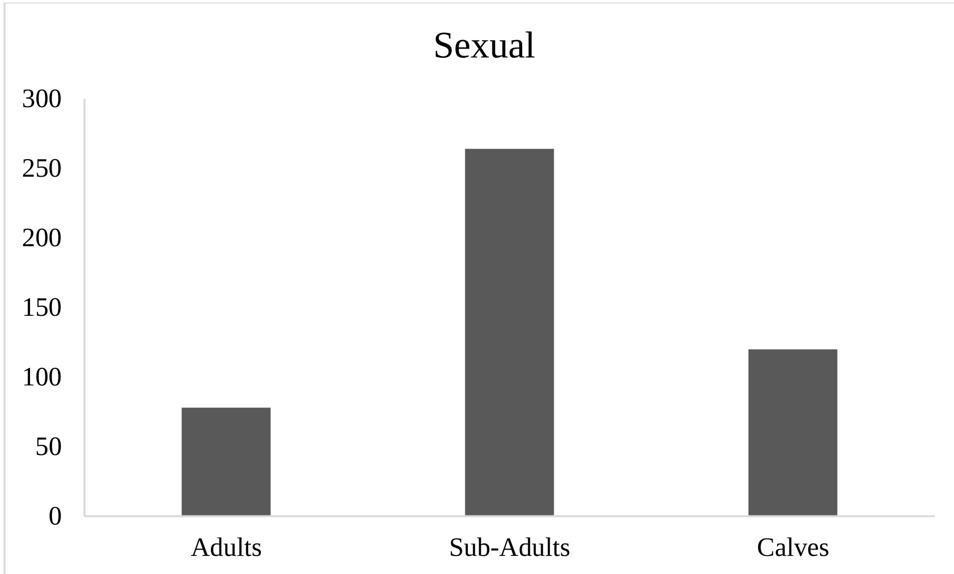

Figure 10. Frequency of overall mouthing behaviors in the sexual context by age-class.

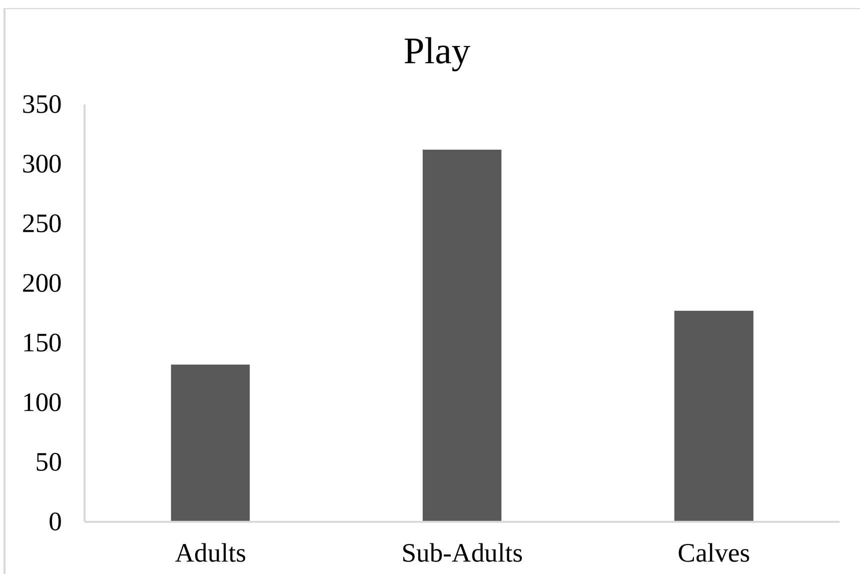

Figure 11. Frequency of overall mouthing behaviors in the play context by age-class.

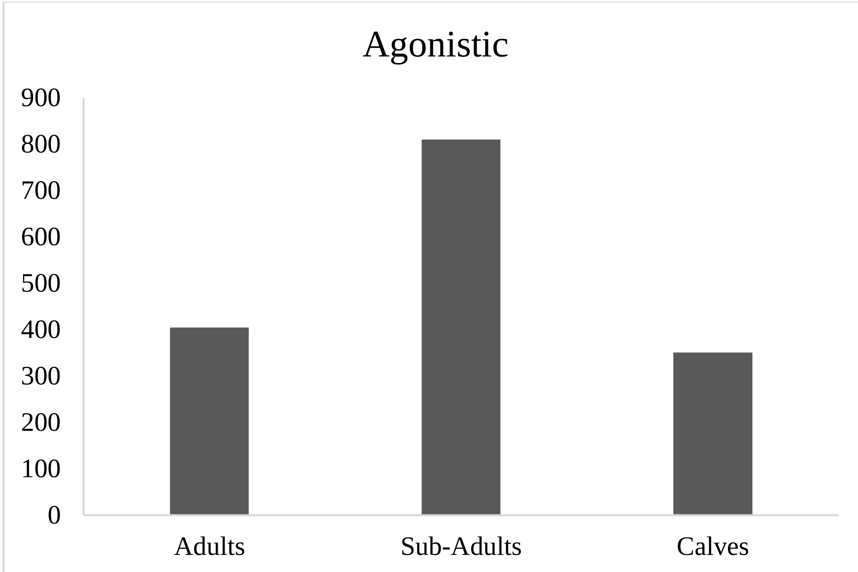

Figure 12. Frequency of overall mouthing behaviors in the agonistic context by age-class.

Sex-Differences Analyses

Loglinear analyses revealed that there was an overall main effect based on sex, mouthing type, and behavioral context. K-way effects were non-significant for a 3-way interaction, indicating it should be removed ($\chi^2(9) = 15.20$, K = 3, $p = 0.85$). Interactions between two variables (mouthing type*sex; behavioral context*sex) were significant ($p < 0.01$) and identified for subsequent chi-square analyses between each 2-way interaction.

There were no overall significant differences between the frequency of mouthing behavior type between males and females ($\chi^2(3, N = 4{,}516) = 3.39$, $p = 0.34$). Because there were no conventionally significant results, it was prudent to conduct exploratory analyses to determine potential directional differences based on descriptive statistics (Figures 13 – 16). Overall males engaged in more mouthing behaviors compared to females. Sixty-eight percent of open mouth displays (*n* = 2,925), 68% of mouthing (*n* = 137), 86% of bite (*n* = 19) and 70% of jaw clap (*n* = 26) were exhibited by males compared to the 32% of open mouth displays (n = 1,361), 32% of mouthing (n = 63), 14% of bite (n = 3), and 30% of jaw claps (n = 11) in females.

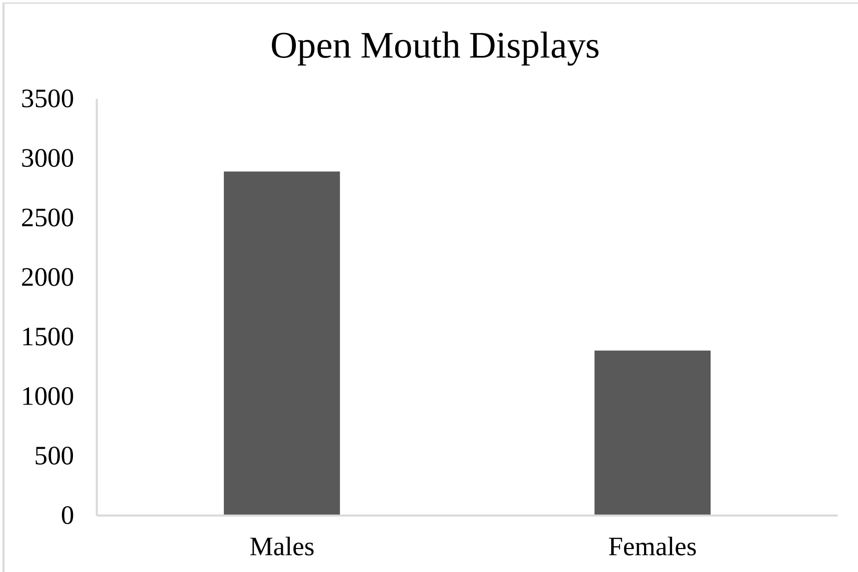

Figure 13. Frequency of open mouth displays by sex.

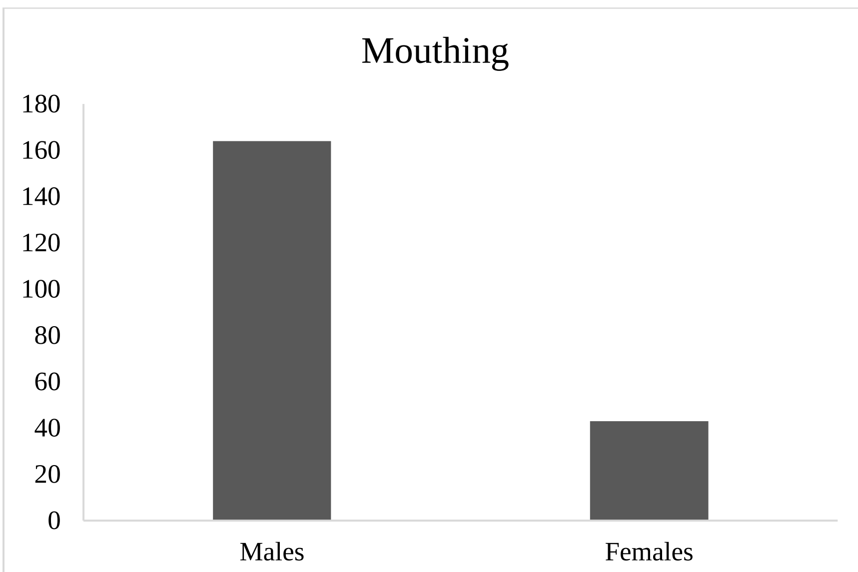

Figure 14. Frequency of mouthing behavior by sex.

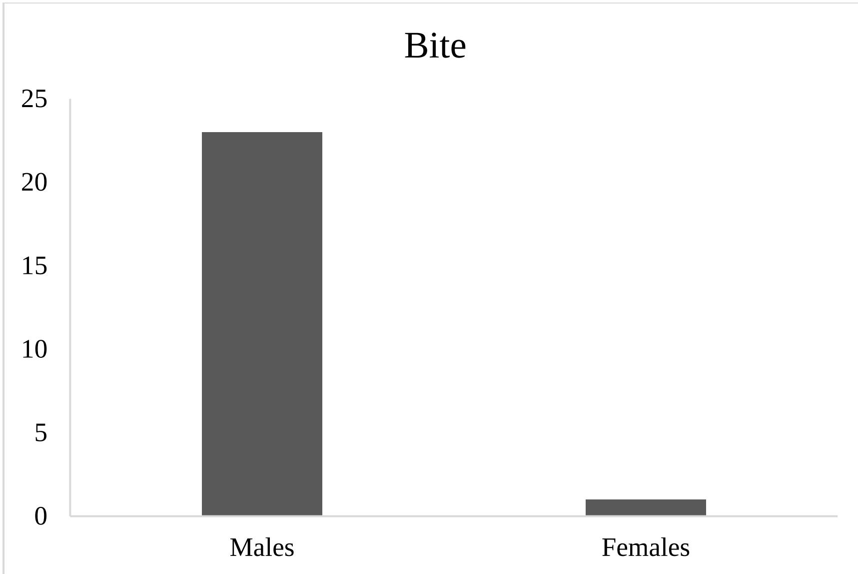

Figure 15. Frequency of bite behavior by sex.

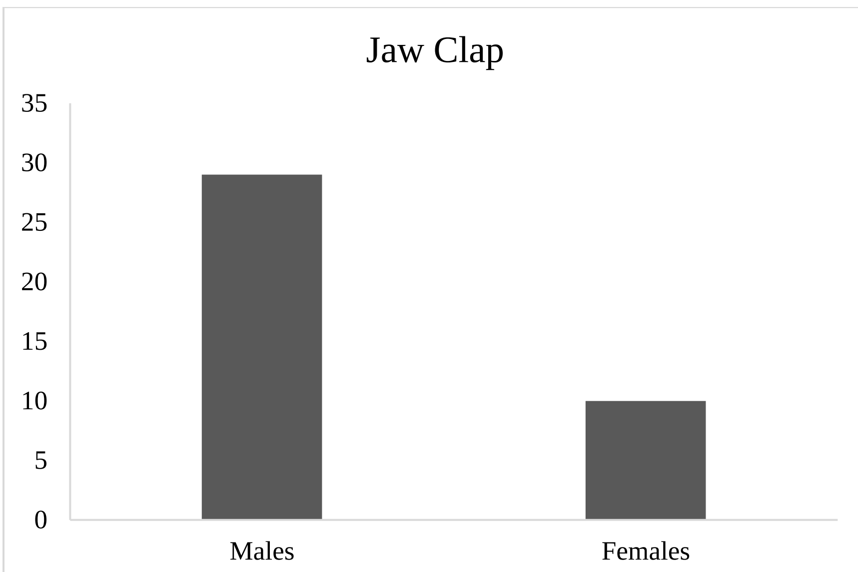

Figure 16. Frequency of jaw-clap behavior by sex.

A Chi-square test of independence was calculated comparing the frequency of mouthing behaviors exhibited in each context across sex for all dolphin subjects (Figure 17). A significant interaction was found ($\chi^2(3, N = 4{,}516) = 13.28$, $p = 0.04$). Mouthing behaviors exhibited by males ($n = 1{,}304$, Std. Residual = 0.7) accounted for 70% of all affiliative mouthing behaviors observed, compared to 30% of female affiliative mouthing behaviors (*n* = 569, Std. Residual = -1.00). For all sexual mouthing behaviors, males exhibited the highest frequency, accounting for 71% of the behaviors observed (*n* = 335, Std. Residual = 0.70), compared to 29% for females (*n* = 137, Std. Residual = -1.00). For all play mouthing behaviors, 71% were exhibited by males (*n* = 445, Std. Residual = -0.80), compared to 29% for females (*n* = 181, Std. Residual = -1.20). Mouthing behaviors in the agonistic context group were also most frequently observed by males (*n* = 1,023, Std. Residual = -1.60) accounting for 65% compared to the 35% observed by females (*n* = 551, Std. Residual = 2.4).

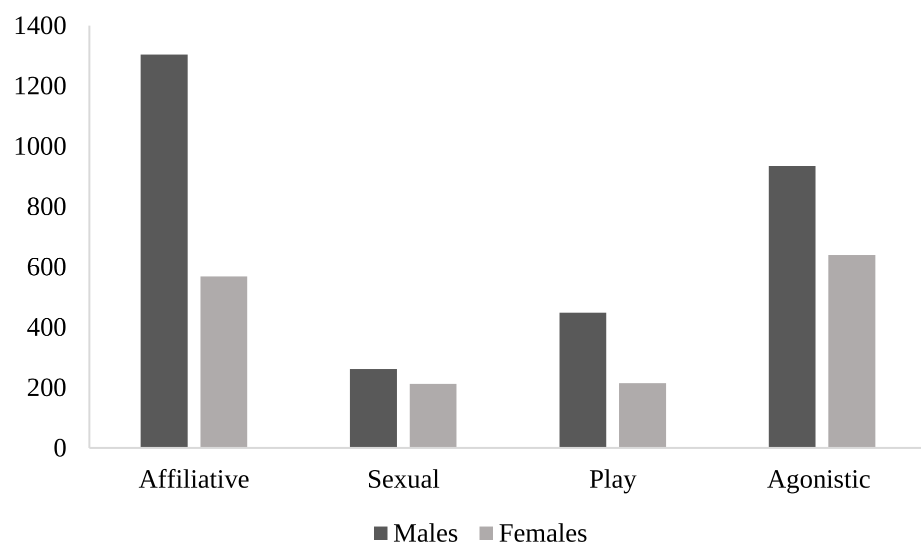

Figure 17. Overall frequencies of mouthing behaviors in each context by sex.

Begin a new chapter here.

CHAPTER IV – DISCUSSION

The goals of the current study were to 1) identify if mouthing behaviors were observed in other contexts besides aggression. 2) identify trends in mouthing behavior expression across different contexts based on sex and age-class differences. Specifically, the four contexts of affiliation, sexual, play, and agonistic emerged and were defined using concomitant behavioral analyses, a methodology similarly observed in the primate literature (e.g., Waller & Dunbar, 2005 DeMarco & Visaberghi, 2007; Visalberghi et al., 2006). The study also revealed significant differences among sex and age-class for the type of mouthing behavior exhibited (i.e., open mouth display, mouthing, bite, and jaw clap), and the observed context (i.e., affiliative, sexual, play, agonistic). Furthermore, the surrounding behaviors immediately preceding and following a focal mouthing event appeared to serve an important role as signals to help communicate the non-threatening use of mouthing behaviors across these different contexts. This initial empirical evidence supports the notion that while mouthing behaviors can serve an aggressive/agonistic function, they may serve a role in sexual, affiliative, and play contexts as well.

Open mouth displays occurred markedly more frequently than all other mouthing behaviors. Each of the four focal mouthing behaviors (i.e., open mouth display, mouthing, bite, and jaw clap) were present across all contexts (i.e., affiliative, sexual, play, and agonistic). Bites and jaw claps were infrequently observed compared to open mouth displays and mouthing, and there were extremely few occurrences of contact-aggression (i.e., ram) observed in the dataset. Both behaviors were retained in the model due to their established use as an index of aggression (e.g., Myers, Herzing, & Bjorklund, 2017; Myers & Overstrom, 1978; Overstrom, 1983; Scott et al., 1995). While it was hypothesized that bite and jaw clap behaviors would only be exhibited in the agonistic context, the results showed that bite and jaw clap were present in each of the four context groups. This result, however, is limited in scope due to the infrequent sample size for these focal behaviors. Possible explanations for this result could be attributed to bite and jaw clap being utilized for a non-threatening function in play or affiliative contexts. Bites and jaw claps observed in the sexual context could be attributed to sexual coercion or dominance related functions, discussed in detail further in the discussion. It also was interesting to note that the majority of bite behaviors were exhibited in the affiliative context, predominantly by sub-adults and calves interacting with adult females. However, the bites in the affiliative context were immediately followed by contact swim and pectoral fin contact, which is thought to function to repair relationships during bond formation and/or discipline exchanges (e.g., Weinpress & Herzing, 2015; Yamamoto et al., 2015). It is also probable that these bite occurrences were an attention-seeking behavior, used by younger animals to get attention from mothers or older playmates. Nevertheless, further analysis with increased sample size for bite and jaw-clap are necessary in order to determine the validity of this contextual data being applicable to these behaviors. Due to the small sample size for bite and jaw-clap, the majority of the context interpretation will focus on the open mouth displays and mouthing.

The emergence of an agonistic context provides further support that open-mouth displays, whether static or sparring, do communicate information relevant to advertising threat or aggression under certain environmental and social conditions (e.g., Campagna, 2009; Myers & Overstrom, 1978; Overstrom, 1983), but are not limited to this one function. Significant behaviors comprising the agonistic context included approach, hit, chase, abrupt head movements, being the recipient of mouthing behaviors from other conspecifics, and engaging in mouthing behaviors immediately before and following a focal event. In particular, sequences of aggressive behaviors and mouthing behaviors occurring in rapid succession and escalating to a highly aggressive event (i.e., ram) has been previously described in various social interactions between bottlenose dolphins (e.g., Myers & Overstrom, 1978, Overstrom, 1983, Samuels & Gifford, 1997). Sub-adults in particular were significantly more likely to engage in open mouth displays, mouthing, bite, and jaw claps as well as exhibited the highest frequencies of mouthing behaviors across all four contexts (i.e., affiliative, sexual, play, and agonistic). Males exhibited more mouthing behaviors across all contexts compared to females. The sex and age-class of the mouthing dolphin were both thought to predict dominance and directionality of aggressive encounters (e.g., Cusick & Herzing, 2014); where the dominance status of an individual can change frequently during social agonistic behavioral exchanges (Yamamoto, Ishibashi, Yoshida, & Amano, 2016). Dominance reversals, where a submissive individual becomes the dominant individual during a social exchange, can transpire within single encounters or as a result of several interactions occurring over time (Cusick & Herzing, 2014; Samuels & Gifford, 2007). Across taxa, individuals in the social hierarchy that occupy similarly ranked positions are more prone to dominance reversals, creating unstable relationships and subsequently, an increased frequency of agonistic interactions (Cusick & Herzing, 2014; Heitor & Vicente, 2010; Kitchen, Cheney, & Seyfarth, 2005; Rychlik & Zwolak, 2006; Yamamoto et al., 2016). The male sub-adults in the study population occupy mid-ranked and lower positions in the hierarchy (Frick, 2016); suggesting that the prevalence of open mouth displays in the agonistic context may be relevant for communicating information related to dominance/social rank.

The function of agonistic behavior varies across taxa, but is associated with a variety of costs for both the actor and the recipient depending on the behavior (Aureli et al., 2002; Campagna, 2009). Display behaviors in an agonistic context (i.e., open mouth displays, S-posture) do not require high energy expenditures nor cause immediate harm to the recipient. Conversely, a ram behavior in an agonistic context requires a greater energy expenditure for the actor and can cause severe harm or even death to the recipient (Campagna, 2009). The extremely high frequency of open mouth displays in an agonistic context compared to all other mouthing behaviors could be attributed to the decreased energy expenditure associated with the display behavior as opposed to the contact behaviors (i.e., mouthing and bite) and the high-energy jaw clap threat. Agonistic open mouth displays may sufficiently communicate or advertise threat to other conspecifics to avoid further high-energy agonistic behavioral events such as rams, which were infrequently observed.

The mouthing dolphin (i.e., actor/initiator) was frequently the recipient of pectoral fin rub and rub behaviors from other dolphins during agonistic mouthing exchanges. Studies of conflict management amongst group-living species suggest that submissive behaviors in response to contact aggression or the threat of aggression may reduce the likelihood of being the recipient of future aggressive behaviors (e.g., de Boer, Overduin-de Vries, Louwerse, & Sterck, 2013; Yamamoto et al., 2015). In bottlenose dolphins, assessments of post-conflict affiliative and submissive behaviors directed by the recipient to the actor (i.e., aggressor) decreased future aggression and possibly served a reconciliatory function (Yamamoto et al., 2016). Furthermore, body contact (e.g., pectoral fin rubbing) occurred more frequently post-aggression (i.e., immediately following an aggressive exchange), suggesting physical contact and rubbing may help reduce tension and repair relationships post-aggression (Tamaki, Morisaka, & Taki, 2006). Similarly, discipline exchanges between mothers/alloparents and calves may often be followed by contact swims (Hill, Greer, Solangi, & Kuczaj, 2007; Weinpress & Herzing, 2015; Yamamoto et al., 2015, 2016). Contact swims can be defined as dolphins swimming close together while maintaining almost constant contact of one body part to another between dyads (Dudzinski, 1996; Kuczaj & Frick, 2015). In the present study, post-agonistic mouthing events frequently appeared to elicit rubbing and contact behaviors directed toward the mouthing dolphin by the recipient, suggesting they may serve to repair the relationship between individuals or mitigate being the recipient of further agonistic behaviors.

Swim behaviors related to synchronicity between multiple individuals significantly loaded in the agonistic context (i.e., group swim). The particular context observed for dolphins engaging in synchronized group swims can change multiple times during a single encounter, depending on the group composition (Connor, Mann, & Watson-Capps, 2006; Fellner, Bauer, Stamper, Losch, & Dahood, 2012; Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010) Synchronicity has been observed as a mitigating factor in aggressive encounters involving spotted dolphins (Cusick & Herzing, 2014). The authors suggest that spotted dolphin group synchronization may be advantageous during aggressive exchanges with the larger bottlenose dolphins. During synchronized aggressive exchanges, display behaviors (including open mouth displays) have been significantly exhibited by bottlenose dolphins (Myers et al., 2017). In the present study, many of the individuals that comprised group swim groups were sub-adults and calves of various body lengths and size, many of which were notably smaller in physical size than the more dominant adult males, who were not as frequently members of group swim. It is possible that synchronizing swim behaviors amongst several individuals that are younger and are smaller in stature increases the likelihood of exhibiting open mouth displays in an agonistic context; a pattern similarly observed in cross-species interactions where smaller cetaceans engage in more confrontational behaviors when in synchronized groups (e.g., Cusick & Herzing, 2014; Myers et al., 2017).

Approximately 10% of all observed mouthing behaviors were in the sexual context. In this context, open mouth displays may communicate submissive and dominance information, as seen in several primate species (e.g., de Boer et al., 2013; DeMarco & Visaberghi, 2007; Visalberghi et al., 2006). The context of male-female sexual interactions can be both agonistic and sexual simultaneously, as evidenced by several reports of sexual coercion in bottlenose dolphins (e.g., Scott et al., 2005). Sexual coercion involves male aggression directed towards fecund females to increase their likelihood of successful copulation and decrease the likelihood of other males intervening, albeit at some cost to the female (e.g., Scott et al., 2005; Smuts & Smuts, 1993). Such male sexual aggression is observed more frequently in promiscuous species like bottlenose dolphins, where females mate with multiple partners throughout their lifetime (Connor, Richards, Smolker, & Mann, 1996). In spinner dolphins, large male mating groups can exhibit open mouth displays and biting towards other males when competing for access to females (Silva, Silva, & Sazima, 2005) Male alliances may even cooperate to sequester fertile females to increase their chances for mating success (Connor et al., 1992).

However, many of the observed sexual exchanges in the study population were between individuals of the same sex, in a possible socio-sexual or sexual play function. In dolphins, Wickler (1967) suggests socio-sexual exchanges serve key functions for establishing and maintaining social relationships amongst males. Such socio-sexual exchanges often occur amongst closely ranked individuals toward the middle or lower end of the hierarchy, suggesting that the prevalence of socio-sexual behaviors may communicate dominance information without the need for highly aggressive behaviors (Mann, 2006). Socio-sexual exchanges may also serve a role in the formation of pair-bonds or alliance membership, due to the role exchange where an actor adopts a dominant position and the recipient a more submissive position (Mann, 2006; Connor et al., 1992).

Open mouth displays have been discussed only recently as being indicative of showing interest, excitement, and/or surprise in play and other non-aggressive contexts (Dudzinski, 1998; Lilley et al., 2018; Moreno, 2017); as well as soliciting interactions with other conspecifics (i.e., mating, play). Curiosity/showing-interest responses in bottlenose dolphins have been described as the dolphin attending to novel stimuli and releasing bubble bursts accompanied by open mouth displays (e.g., Clark, Davies, Madigan, Warner, & Kuczaj, 2013; Frick, 2016; Hill et al., 2011). For example, Lilley and colleagues (2018) categorized curiosity responses to surprising stimuli, presenting captive bottlenose dolphins with several stimuli that underwent a transformative change.

Open mouth displays observed by the subjects were concluded as not indicating aggression. Rather, the open mouth display response was suggested to signal surprise or showing interest to the novel stimuli.

The visual appearance of an open mouth display may also indicate interest during social play exchanges. Play is notoriously difficult to define, but can be described as repeated functional behaviors used non-purposefully in a relaxed or positive setting, and is rewarding for the animals involved (Burghardt, 2005). In the present study, sub-adults and calves both exhibited higher frequencies of mouthing behaviors in the play context compared to adults, which is consistent with previous findings that state developmentally (Burghardt, 2005; Hill & Ramirez, 2014), peak play periods begin shortly after infancy and last into the early sub-adult period (Bekoff & Byers, 1998; Burghardt, 2005; Hill & Ramirez, 2014; Pellis & Pellis, 2013; Power, 2000; Worch, 2012). Play behaviors in dolphins are thought to indicate the ontogeny of problem solving skills through spontaneous imitation and observational learning of play behaviors by calves and juveniles (Kuczaj & Yeater, 2006; Kuczaj & Horback, 2012). Individuals that are more bold and curious tend to be more likely to have their behavior mimicked and modeled by other dolphins in a given social group (Kuczaj et al., 2006). While mouthing behaviors used to interact with objects were not analyzed presently, future research aims to identify how/if a play context still emerges when dolphins direct mouthing behaviors on objects rather than in social exchanges.

High-energy play behaviors in a variety of taxa utilize similar behaviors that serve a functional purpose in other contexts (i.e., sexual, aggressive, predatory). Social play is thought to help with the development of an animals' motor skills and promote flexible and cognitive thinking. Additionally, social play provides an opportunity for younger cetaceans to practice and develop the use of functional behaviors in ‘safe’ social situations while simultaneously forming bonds that may turn into alliances or future relationships (e.g., Bekoff & Byers, 1998; Burghardt, 2005; Hill & Ramirez, 2014). Behaviors that significantly loaded with high probabilities to the play context included group social ball, chase, bubble burst, and tactile behaviors. Animals rely on visual signals to communicate to other conspecifics during play that the behaviors are non-aggressive and non-threatening (Palagi & Mancini, 2011). For example, silent bared teeth display in tonkean macaques (*Macaca tonkeana*) that immediately preceded an open mouth signaled to the playmate that the interaction was playful (i.e., open mouth play face display), and that the open mouth was not in preparation for a bite (Pellis, Pellis, Reinhart, & Thierry, 2011). While dolphins and other cetacean species cannot physically manipulate their facial muscles to form diverse facial expressions like primate species can, it is possible that visual behavioral signals used by cetaceans can help communicate the non-threatening use of open mouth displays. For example, it is possible the prevalence of bubble burst behaviors immediately preceding mouthing behaviors at the onset of a play exchange may be similarly used to indicate excitement or interest surrounding a social play bout (i.e., Moreno, 2017) rather than aggression, supporting the assignment of “play” to open mouth displays and mouthing behaviors observed in this context.

Affiliation was the most frequent context observed for mouthing behaviors. The high frequency of affiliative mouthing behaviors is not consistent with much of the previous literature, due to the predominant hypothesis that mouthing behaviors served only an agonistic function. However, the use of behaviors of the mouth for communicating affiliation has been well documented in several species of primates. For example, the silent bared teeth display involves the actor retracting its lips to expose the teeth with the jaws open or closed, and it is reported in several species of macaques, chimpanzees, and siamings (Preuschoft & Van Hooff, 1997; Thierry et al., 2000). In macaque species with relaxed dominance systems, the silent bared teeth display is used as a visual signal to initiate a peaceful social exchange, independent of the dominance status of the actor (Bout & Thierry, 2005; Petit et al., 1997; Thierry et al., 2000). However, the open-jawed variant of the silent bared teeth display is almost indistinguishable from the relaxed open mouth display seen during play; it is hypothesized that this overlap mirrors the behavioral overlap between smiles and laughter in humans (Van Hoof, 1972). Concomitant behavioral analyses of silent bared teeth display in mandrills (*Mandrillus sphinx*) also revealed that this display served an affiliative function in this species, and it was immediately preceded and followed by other behaviors indicative of affiliation, play, or mating (Bout & Thierry, 2005). While dolphins and other cetaceans have more limited facial movements, it is likely that similar to primates, mouthing behaviors may serve an affiliative function that can only be revealed through concomitant behavioral analyses.

Positive behaviors known to be associated with affiliation in dolphins, including pair swim with contact, were significant and emerged with the highest probabilities for the affiliative context for mouthing displays. Contact swim is a behavior previously identified affiliative in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*; Connor et al., 2006). Contact swimming involved females maintaining bodily contact while traveling in the same direction in a synchronous manner. This behavior was thought to help decrease the risk of herding and harassment by other males in their social group (Connor et al., 2006). Male dolphins have also been observed engaging in contact swim behavior. Personality assessments utilizing a coding methodology of the same population used in the current study revealed high trait scores of propinquity (i.e., contact-seeking) with other dolphins (Frick, 2016). Older males with high coefficients of association that were identified as an allied pair were often observed engaging in pair swim with contact, suggesting this behavior served a role in relationship formation and/or maintenance. In the present study, other identifying behaviors for the affiliative context included abrupt head movements. While abrupt head movements are more commonly associated with agonistic context and play, primates have noted similar reactions accompanying affiliative mouth behavioral displays in the form of 'head shaking.' The head shaking behavior in conjunction with the affiliative mouthing display is thought to be assertive in this context, and serve to reassure the recipient that the actor's intent is non-threatening (Bout & Thierry, 2005.) In dolphins, these head movements may serve a similar assertive or reassuring function, but further research specifically focusing on abrupt head movements in relation to mouthing behaviors is needed.

For all focal mouthing types (i.e., open mouth display, mouthing, bite, and jaw clap) and all contexts observed (i.e., affiliative, sexual, play, and agonistic) sub-adult males exhibited the highest frequencies for all behaviors across all contexts. These high frequencies can be attributed to the developmental stages of these animals for the behaviors associated with play, socio-sexual contact, and aggression. Sub-adults in the study population (i.e., Frick, 2016) are mid-ranked in the hierarchy, which is indicative of conflict due to the instability from the animal defending its current position or attempting to advance to a higher status (e.g., Scott et al 1995). Similarly, sub-adult males exhibited high frequencies of socio-sexual contact with other males, which is also thought to communicate dominance information via role exchange between individuals without the need for aggression (e.g., Mann, 2006). Regarding the high frequencies of sub-adult mouthing displays in the play context, dolphins are more likely to engage in novel play, and are considered important to the transmission of play within a social group (Kuczaj & Eskelinen, 2014). In the present study, younger animals (i.e., sub-adults) were more likely to engage in mouthing behaviors in the play context compared to adults, indicative of high-energy social play bouts. This mirrors the developmental trend in most species where after an initial peak, play is less likely to occur during significant physical development and then increase during the juvenile or sub-adult period and subsequently decreasing in adulthood (e.g., Burghardt, 2005).

Future Directions

Future directions for this research include analyzing the sex and age-class of dyadic interactions between actor and recipient dolphins for each mouthing behavior type across all context groups, to identify relationship symmetry between various dyads. Additionally, actor and recipient exchanges will be analyzed to determine if unilateral or bilateral social exchanges are more prevalent for each of the four mouthing types based on the context the mouthing behavior is exhibited. I also would plan to conduct acoustic analyses of group-level vocalizations present during the same concomitant time periods (i.e., ± 3 sec) for open mouth displays, mouthing, bite, and jaw clap to identify patterns in vocalizations present based on the context of the mouthing behavior, as well as noted differences in vocalizations present based on the context observed. The current study solely focused on social mouthing exchanges (i.e., between conspecifics), so future directions will also include analysis of the additional 5,000 mouthing events that were recorded with their antecedents and consequences (± 3 sec) that were directed toward an object or a person. This will allow for comparisons of how contexts present may be similar or different based on if the mouthing behaviors are directed toward other dolphins or directed toward an object or person.

Conclusions

The results from this study provide initial empirical investigation and initial evidence to identify contexts for social mouthing exchanges beyond aggression. Identifying and defining the key behaviors which comprise the context groups of affiliative, sexual, play, and agonistic surrounding mouthing behaviors will inform future research that utilizes open mouth displays, mouthing, bite, and jaw claps in their analysis, to allow for a more accurate interpretation of these behaviors function. The methodology and statistical analyses used to obtain these context groups and objectively assign all focal events to a context group is also remarkable in its efficiency. Its application in the current study may serve as a model for other longitudinal analyses that seek to determine the context and function of a given behavior. The use of concomitant analyses is a useful tool that helps comprise a more complete picture with contextual information for the target behaviors. Future research regarding bottlenose dolphin social behavior or cognitive abilities should account for the various contexts that exist and affect the interpretation of the function of open mouth displays, mouthing, bite, and jaw claps.

APPENDIX A – OPERATIONAL DEFINITIONS OF ALL BEHAVIORS CODED

If there are tables included in your Appendices you may use the same formatting as seen in the other sections of your document. If you are inserting a .pdf, see instructions in the Guidelines. Tables, figures, etc. in the Appendix will need to have the "Appendix style" applied to it. See USM Guidelines for more details. If you had to have IRB/IACUC approval, your letter must be put into the appendix. Also, you should place any permissions that you had to obtain in the appendix.

Table A1.

Focal Mouthing Events

CODE	**MOUTHING TYPE**	**OPERATIONAL DEFINITION**
OPM	Open Mouth	Dolphin separates its jaws often exposing teeth
MOU	Mouthing	Dolphin has mouth around a conspecific's body, object, or person, but is not biting down
BIT	Bite/Rake	Dolphin closes mouth with force around another dolphin on any part of the body (bite), or rubs/slides its jaw, with teeth, along a conspecific
JAC	Jaw Clap	Dolphin produces a loud popping sound coupled with a fast open and close of the mouth

Adapted from Dudzinski (1996); Kuczaj & Frick (2015); Overstrom (1983).

Table A2.

Operational Definitions of Behaviors Coded

CODE	**BEHAVIOR**	**OPERATIONAL DEFINTION**
APP	Approach	Dolphin quickly another dolphin and an interaction between them occurs ** starts with the turn or directed movement towards another conspecific, ends with the interaction
APR	Approach Recipient	Dolphin is advanced upon by another dolphin and an interaction occurs

CHS	Chase	Rapid and persistent pursuit of another dolphin, **during a chase dolphins are not members of the same group
AVF	Avoid/Flee	Abrupt, rapid, and immediate departure in response to action of another dolphin, ****during a chase, dolphins are not members of the same group
AVH	Abrupt Vertical Head Movement	Dolphin moves head up and down in quick jerking movements
AHH	Abrupt Horizontal Head Movement	Dolphin moves head from left to right in quick jerking movements
BBB	Bubble Burst	Dolphin produces large bubble/bubbles from blowhole similar to those produced by scuba equipment
BBT	Bubble Trail	Dolphin produces a series of small bubbles from blowhole that form a trail
GSB	Group Social Ball	Three or more dolphins swim around each other and appear to be “wrestling”, such that it is extremely difficult to identify the individual behaviors in which each animal is engaged. Dolphins are categorized as being members of the same "group"
HIT	Hit	Dolphin contacts another dolphin using rostrum or fluke in a quick and aggressive manner
HTR	Hit Recipient	Dolphin is contacted by another dolphin's rostrum or fluke in a quick and aggressive manner
HRD	Herd	Dolphin is behind another dolphin and directing the second dolphins movement
HRE	Herd Recipient	Dolphin is in front of another dolphin and its movement is being directed by second dolphin
HSC	Head Scanning	Dolphin is moving head quickly and laterally side to side (often while echolocating)
ODG	Orient to Dolphin in a Different Group	Dolphin turns head to other dolphin in a different group (more than 1 dolphin away, not synchronous behavior, approx 3.5m)
OSG	Orient to Dolphin in the Same Group	Dolphin turns head towards another dolphin in same group (lee than 1 dolphin away, synchronous behavior, approx 3.5m)
OTC	Orient to Camera	Dolphin turns head to camera
OTP	Orient to Person	Dolphin turns head towards a human
OTO	Orient to Object	Dolphin turns head towards an object (Record the object)

PET	Pet	Pectoral fin to pectoral fin rubbing where active movement between pectoral fins is observed
PRB	Pec Rub	Dolphin actively rubs another's body with its pectoral fin
PRR	Pec Rub Recipient	Dolphin is rubbed with another dolphin's pectoral fin actively
RUB	Rub	Dolphin uses a body part other than the pectoral fin to rub against another dolphin in a manner that is not considered sexual contact **NOT the same as pair swim with contact, do not code both
RBR	Rub Recipient	Dolphin is rubbed against by another dolphin's body part other than their pectoral fin in a manner that is not considered sexual contact
SEX	Sexual Behavior	Dolphin is interacting with another sexually as evidenced by genital-genital contact, rostrum/fin/other bodily contact with another's genitals, or an erection and copulation attempt
TCT	Tactile	Dolphin **briefly** contacts (touches) another dolphin in a manner that is not otherwise listed (Record type of contact)
TCR	Tactile Recipient	Dolphin is **briefly** contacted (touched)by another dolphin in a manner that is not otherwise listed (Record type of contact)
OPM	Open Mouth	Dolphin separates its jaws often exposing teeth
OPR	Open Mouth Recipient	Focal Dolphin is the recipient of another dolphin that separates its jaws often exposing teeth
MOU	Mouthing	Dolphin has mouth around a conspecific's body, or around an object, but is not biting down
MOR	Mouthing Recipient	The focal Dolphin has another dolphin's mouth around its body but the dolphin is not biting down on it
BIT	Bite/Rake	Dolphin closes mouth with force around another dolphin on any part of the body (bite), or rubs/slides its jaw, with teeth, along a conspecific
BTR	Bite/Rake Recipient	Another dolphin closes mouth with force around the focal dolphin
JAC	Jaw Clap	Dolphin produces a loud popping sound coupled with a fast open and close of the mouth
JAR	Jaw Clap Recipient	Another dolphin produces a loud popping sound coupled with a fast open and close of the mouth at the focal dolphin
PSC	Pair Swim with Contact	Dolphins swimming close while maintaining contact of one body part to another *NOT the same as rubbing, do not code both
SOS	Solo Swim	Dolphin is swimming alone
PRS	Pair Swim	Dolphin is swimming synchronously in same direction with another that is within a dolphin-body-length (approx. 2.5 m)
GRS	Group Swim	Three or more dolphins are swimming synchronously in same direction within a dolphin-body-length (approx. 2.5 m) of each other, OR behaving synchronously

N/A	Not applicable	The focal dolphin is not on screen

Adapted from Dudzinski (1996); Kuczaj & Frick (2015); Overstrom (1983).

Table A3.

Operational Definitions for Target of the Mouthing Behavior

CODE	**Mouthing Direction**	For Open Mouth: Rostrum must be pointed directly at/inclined toward the target (without reasonable doubt). For Mouth and Bite/Rake: Target must be inside dolphin's mouth.
UNK	Unknown	Mouthing behavior is directed towards unknown
SGR	Same Group	Mouthing behavior directed towards dolphin in same group
DGR	Different Group	Mouthing behavior is directed at dolphin in different group
CAM	Camera	Mouthing behavior is directed at the camera
PER	Person	Mouthing behavior is directed at a person
OBJ	Object	Mouthing behavior is directed at an object

Adapted from Dudzinski (1996); Kuczaj & Frick (2015); Overstrom (1983).

APPENDIX B – IACUC Approval Letter

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI.

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
118 College Drive #5116 | Hattiesburg, MS 39406-0001
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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

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

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

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

____________________________ _____October 9, 2014_____________

Frank Moore, Ph.D. — Date
IACUC Chair

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