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The Development of Socio-sexual Behavior in Beluga Whales (*Delphinapterus leucas*)

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THE DEVELOPMENT OF SOCIO-SEXUAL BEHAVIOR IN BELUGA WHALES
(DELPHINAPTERUS LEUCAS)

by

Malin Katarina Lilley

A Dissertation
Submitted to the Graduate School,
the College of Education and Human Sciences
and the School 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

The reproductive success of the beluga whale is critical for a species facing extinction in its endangered Cook Inlet, Alaska population. To date, little is known about the mating behavior of these whales in wild populations. On the other hand, observations of beluga whales in human care allow researchers to better understand many aspects of their daily lives and life histories that are difficult to assess in wild populations. Thus far, a catalog of socio-sexual behavior has been established based on observations of belugas; however, the developmental trajectory of socio-sexual behavior is not well-understood. The present study explored how socio-sexual behavior developed in beluga whales under human care by recording the behavior of 5 belugas between ages 4 through 10 and coding for socio-sexual behavior. Overall, the presence of young male conspecifics was the most influential predictor of whether or not the subjects engaged in socio-sexual behavior. The subjects of the present study were also more likely to be involved in socio-sexual behavior as they matured and were more likely to be involved if they were male. In contrast, the presence of environmental enrichment devices (EEDs) did not affect the prevalence of socio-sexual behavior. Additionally, specific socio-sexual behaviors, including horizontal s-postures and pelvic thrusts, increased in prevalence throughout development. This information is important for the management of beluga whale populations both in human care and in the wild. Understanding that social group composition may contribute to the development of socio-sexual behavior, which in turn may influence the reproductive success of beluga whales, lays the ground work for future research of socio-sexual behavior in wild belugas. Furthermore, because socio-sexual behavior composes a relatively large portion of a beluga's activity budget and the

majority of the time spent socializing, it is likely crucial for social bonding and well-being in belugas.

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DEDICATION

This dissertation is dedicated to Rehman and my family. Thank you for believing in me!

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CHAPTER I – INTRODUCTION

Socio-sexual Behavior in Non-cetacean Species

Although the vast majority on sexual behavior in non-human species has focused on reproductive purposes, there is a relative dearth of research on the non-reproductive, or socio-sexual behaviors, of nonhuman animals (Baily & Zuk, 2009). Additionally, much of the existing research in this domain has focused on small animals, with little research focusing on the socio-sexual behaviors of larger mammalian species (Hill, Artz, & Lopez, 2014). Given that many of these larger species are categorized as threatened, a better understanding of socio-sexual behaviors in these populations may contribute to these species' conservation.

Socio-sexual interactions involving two individuals of the same sex occur in a wide range of species (Baily & Zuk, 2009). In birds, male-male socio-sexual behavior occurs across all types of mating systems (MacFarlane, Blomberg, Kaplan, & Rogers, 2007). A survey of same-sex sexual behavior in mammals found that same-sex interactions are quite common across a variety of species as well (Dagg, 1984). Proposed functions for same-sex sexual behavior include creating and maintaining dominance hierarchies, engaging in social play or aggressive behaviors, and acting on sexual excitement or a desire for physical contact. In rabbits, female-female mounting behavior helps to establish and maintain the dominance hierarchy, with the mounting rabbits becoming more dominant over the mountees (Albonetti & Dessi-Fulgheri, 1990). In contrast, determining dominance in relationships is not necessarily a function of male-male mounting; rather, in deer, such behavior is hypothesized to be due to a side effect of excitement (Bartos & Holeckova, 2006). Research supports the claim that for feral cats,

many male-male mountings are likely due to sexual frustration (Yamane, 2006). Even insects are reported to engage in same-sex copulation, the function of which varies by species but ranges from reducing the energetic and physiological ability of other males to successfully mate with females, to depositing sperm in another male so that sperm can fertilize a female via another male's copulations (i.e., sperm competition; Bailey & Zuk, 2009). Given the above examples, it is important to remember that precocious sexual behavior and sexual interactions involving two individuals of the same sex may have different origins and different functions that are unique for individual species. For some species, same-sex socio-sexual behavior may help to establish dominance hierarchies, while same-sex socio-sexual behavior in other species may be the result of an increase in overall sexual excitement or a strategy to increase reproductive fitness.

Even among primates, there is a wide range of proposed functions for same-sex socio-sexual behavior. Sexual gestures have been reported as part of ritualized greetings for baboons (Smuts & Watanabe, 1990), while genital contact between female bonobos is used for reconciliation and tension reduction after conflicts have occurred or in situations where a food source could be monopolized (Hohmann & Fruth, 2000). Same-sex mounting behavior in mountain gorillas also seems to be related to maintenance of the dominance hierarchy, but the adaptive function of the mounting behavior is not explicitly clear (Grueter & Stoinski, 2016). When the frequency of non-conceptive sexual behavior was compared for bonobos and capuchins, it was found that socio-sexual interactions were more frequent in the sex that migrated to a new social group (female bonobos and male capuchins) and occurred most frequently in situations where individuals were in socially tense situations (Manson, Perry, & Parish, 1997). Non-copulatory sex in both

bonobos and capuchins could be for practice and social facilitation in stressful situations, and, for capuchins only, may function to create paternity confusion (Manson et al., 1997).

Vasey (1995) proposed that same-sex socio-sexual behavior may be the result of an exaptation of reproductive behavior that now has many functions, which include establishing dominance, practice for successful reproduction, helping to reduce tension between individuals, aiding in reconciliation, facilitating the formation of alliances, and reducing the mating success of other conspecifics. In some cases, the reproductive fitness benefits of socio-sexual behavior may be the result of forming positive social relationships with other conspecifics. For example, bonobos use socio-sexual behavior to ease social tension and gain access to food when there are limited supplies, which in turn allows an individual to gain more food resources and thus contributes to that individual's reproductive fitness.

In order to understand how socio-sexual behavior is involved in such social relationships, some studies have focused on species of primates and cetaceans, which have varying types of social structures and complex social interactions between individuals. Monkeys, apes, and dolphins display higher frequencies of same-sex socio-sexual behavior as compared to other species (e.g., reptiles, fish, amphibians), suggesting that a link may exist between the function of socio-sexual behavior for maintaining complex social relationships and higher intelligence (Furuichi, Connor, & Hashimoto, 2014). In particular, these species appear to have more complex and enduring social relationships, which can affect individuals' survival and reproductive fitness. For example, bonobos seem to use socio-sexual behavior to increase group cohesiveness and gain access to food sources, while dolphins form long-term male-male bonds that allow

them to work together to increase mating success by cooperatively mating with and guarding receptive female dolphins (Furuichi et al., 2014). The common factor between these situations is that the species involved have to navigate social relationships to be successful. While these functions of non-reproductive sexual behavior might be driving forces behind the prevalence of the behavior, other functions, such as learning behavior from conspecifics and practice for heterosexual mating, may also be at play but have only been the topic of research in a limited number of species, as discussed below.

Socio-sexual behavior in young animals can be considered a form of motor play. One of the many proposed functions of motor play is that play allows an individual to practice motor skills during a sensitive period of development (Byers, 1998). Burghardt (1998) describes precocious sexual behavior as a form of play in turtles, where the young turtles have more exaggerated and long-lasting displays, though it is not clear what the evolutionary origins and functions of this behavior are.

In some species, there is evidence of more frequent play behavior in young individuals being correlated with more successful reproduction later in life, which supports early play behavior as a means to practice physical and/or social skills. For example, early play behavior in female Belding's ground squirrels is associated with more territorial behavior later in life and also greater success in weaning a litter of offspring (Nunes, 2014). Precocious socio-sexual behavior in spiders is considered a form of play by which both males and females gain experience via non-reproductive sexual behavior before females mature (Pruitt, Burghardt, & Reichert, 2011).

Additionally, male guppies produce courtship behaviors more efficiently if they are able to observe male and female courtship behavior while they are still immature (Guevara-

Fiore, 2012). Male guppies that did not have the opportunity to observe adult courtship behavior were less efficient, attempting more forced copulations and spending less time in courtship displays. Some species, including the guppies described above, are capable of social learning, a topic that has received relatively little attention for its potential influence on mating and socio-sexual behavior. Thus far, the socio-sexual behavior of cetaceans has been described in a handful of species, but the theory of practice and the role of social learning in socio-sexual behaviors have not been explicitly examined for dolphins or other cetacean species.

Cetacean Socio-sexual Behavior

Many species of cetaceans, especially bottlenose dolphins, are known to frequently engage in a variety of socio-sexual behaviors. The reports of socio-sexual behavior in dolphins come from some of the earliest published accounts of dolphin behavior studied in a human care setting (Brown & Norris, 1956; McBride & Hebb, 1948). McBride and Hebb (1948) reported that male bottlenose dolphins engaged in sexual behavior, sometimes with other males, throughout the year. Male dolphins were observed to carry objects with their erect penises and even engage in sexual behavior towards other animals, such as turtles and sharks. Of particular interest in these early observations was the frequency with which males participated in sexual activity with other males. Although often described as copulatory behavior, socio-sexual behavior is not necessarily functionally reproductive (Caldwell & Caldwell, 1977). Two males engaging in pelvic thrusts and intromissions may look behaviorally similar to copulation between a male and female; however, the male-male partnerships appear to be more common and consistent throughout the year.

Long-term studies of wild bottlenose dolphins, primarily those of Shark Bay, Australia, have more extensively explored male-male relationships along with socio-sexual behavior (Connor et al., 1992; Connor, Heithaus, & Barre, 2001; Connor, Smolker, & Beider, 2006; Connor & Krutzen, 2015; Mann, 2006). Male dolphins in Shark Bay develop long-lasting bonds with other males and are commonly found with one or two male conspecifics. These long-lasting relationships are referred to as alliances, as partners of the alliance help to herd and guard ovulating females in order to increase their chance of paternity (Connor et al., 1992). Second and third order alliances form when one or more alliances join together to guard females from other alliances (Connor et al., 2001). The level of synchrony in the behavior of a group of two or more males can be indicative of the strength of the relationship between the individuals (Connor et al., 2006). Individuals who spend more time together likely learn to behave in a similar manner and if reproductive success depends on the synchronization of behavior, this would make the tendency to behave synchronously an adaptive trait (Connor et al., 2006).

Male bottlenose dolphins are reported to mount other males more frequently than they mount female conspecifics, while females are the more common recipient of males' goosing, contact of the genital region using the rostrum (Connor & Krutzen, 2015). Age has also been shown to determine the frequency of socio-sexual behavior, with male bottlenose dolphin calves being the most common actors and recipients of socio-sexual behavior (Mann, 2006). Most socio-sexual relationships appear to be reciprocal, which supports the hypothesis that male-male bonds are formed via socio-sexual behavior and possibly play, though socio-sexual behavior between males may also be a form of practice for later mating with females (Mann, 2006). Bottlenose dolphins in waters near

Japan also have symmetrical socio-sexual relationships where males take turns in the actor and recipient roles and behave in a cooperative manner, indicating that these patterns of behavior occur in multiple populations (Shinohara, 1998).

Recent research on semi-captive bottlenose dolphins mostly aligns with the previous research on socio-sexual interactions in wild populations. Socio-sexual behavior occurs most frequently between male-male pairs, who demonstrate a clear partner preference and have mostly symmetrical relationships (Botero Acosta, 2015; Harvey, Dudzinski, & Kuczaj, 2017). Additionally, the frequency of socio-sexual behavior and partner preferences do not correspond to the dominance hierarchy, which suggests that socio-sexual behavior does not play a role in the formation or maintenance of the dominance hierarchy, but most likely plays a role in bond formation and practice for reproductive copulation (Harvey et al., 2017).

Although bottlenose dolphins are the most commonly studied species in terms of socio-sexual behavior, other species of cetaceans also display some forms of socio-sexual behavior. Reports of these species include socio-sexual behavior of a male Yangtze finless porpoise calf (Xian, Wang, Dong, Hao, & Wang, 2010), male-male socio-sexual behavior of spinner dolphins (*Stenella longirostris*) (Norris & Dohl, 1980), and beluga whale socio-sexual behavior as described below. Additionally, reports of right whale courtship behavior suggest that during reproductive gatherings, there may be some male-male sexual activity that occurs in addition to the males vying for a copulation attempt with a female (Kraus & Hatch, 2001). The authors suggest that male right whales, especially the younger animals in the gathering, are gaining practice and experience with

one another, which might be very valuable in improving the reproductive fitness of the male right whales.

Beluga Socio-sexual Behavior

The socio-sexual behavior of beluga whales has not been extensively studied thus far. As a species, adult belugas do not appear to engage in as many tactile interactions with conspecifics as compared to bottlenose dolphins (Hill, Alvarez, Dietrich, & Lacy, 2016). The difficulty of observing socio-sexual behavior in wild beluga populations may be due, in part, to the lower frequency of tactile interactions between individuals. In a description of beluga whale behavior observed via aerial survey in Cook Inlet, authors reported that they likely observed sexual behavior of the whales (Lomac-Macnair, Smultea, Cotter, Thissen, & Parker, 2015). Unfortunately, the sex, age, and reproductive status of the individual belugas observed were not known, thus the observed behavior could have been play, reproductive behavior, or socio-sexual behavior for a non-conceptive function.

Genetic research on beluga populations migrating in Hudson Bay revealed that males appear to leave their matrilineal groups upon sexual maturity and tend to associate with other males, except during breeding congregations (Colbeck et al., 2013). Similarly, the Beaufort Sea beluga whale population uses the habitat differently based on sex, age, and reproductive status, such that males and females are typically found in separate groups (Loseto, Richard, Stern, Orr, & Ferguson, 2006). Recently, a more complete genetic analysis of North Pacific beluga whales suggested there is limited gene flow between beluga populations, even when populations overlap in habitat use (O’Corry-Crowe et al., 2018). This finding indicates that other populations of belugas are not likely

to contribute via migration to populations that are endangered. Because belugas occupy a broad region with difficult environmental conditions, almost nothing is known about their daily social interactions when not in the breeding areas. Post-mortem examination of beluga reproductive physiology suggests that belugas have a relatively promiscuous mating system, in which sperm competition plays an important role (Kelley, Stewart, Yukowski, Ryan, & Ferguson, 2015), although behavioral observations have yet to support this finding.

In human care, adult male belugas were found to be in proximity to other adult males much more frequently than they were in proximity to adult females (Hill, de Oliveira Silva-Gruber, & Noonan, 2018). In contrast, females were found to swim alone (Hill et al., 2018). Additionally, male belugas showed a seasonal variation in pelvic thrusting towards female recipients but maintained a higher frequency of male-to-male thrusting for the majority of the months in the calendar year (Glabicky, DuBrava, & Noonan, 2010). The higher frequency of male-male socio-sexual behavior is consistent with the higher frequency of male-male socio-sexual behavior in bottlenose dolphins, but the development and possible function(s) of these interactions are not yet understood for belugas.

A catalog of beluga socio-sexual behaviors was established based on video recordings and found to be consistent across several animals housed at three different facilities in North America (Hill, Dietrich, et al., 2015). A previous account of socio-sexual play between adult and immature males reported that open mouths, bubble bursts, and s-postures were common behaviors of socio-sexual interactions, along with the individuals taking turns in each role (Hill & Ramirez, 2014). The s-postures described as

part of socio-sexual behavior occurred while the individual exhibiting the s-posture was positioned horizontally in the water column, which is in contrast to the vertically oriented s-postures displayed as part of agonistic behavior (Horback, Friedman, & Johnson, 2010); however, some behaviors such as open mouth displays, raking, and chases accompany both agonistic and socio-sexual behavior (McKinnon, Dietrich, Aibel, & Hill, 2013). The catalog of socio-sexual behaviors also described socio-sexual interactions as occurring most frequently between an adult male and a juvenile whale. In approximately half of the interactions, the non-initiating whale reciprocated the socio-sexual behavior. Adult females were not frequently observed initiating socio-sexual interactions, yet both female and male juvenile individuals initiated socio-sexual interactions. Additionally, the animals appeared to mirror the partner's behavior in some of the interactions (Hill, Dietrich, et al., 2015).

The behaviors catalogued in this previous study were the focus of observations in the present study and are listed in Appendix A (Hill, Dietrich, et al., 2015). Some of the behaviors included in the socio-sexual repertoire are open mouth displays, lateralized swims, horizontal s-postures, a pectoral fin raised above the water, genital rubs, erections, and pelvic thrusts. Although the socio-sexual behavior of dolphins includes most of these behavioral elements, the lateralized s-posture and raised pectoral fin display seen in beluga behavior does not appear to be a common element in bottlenose dolphin socio-sexual behavior. Interestingly, a lateralized swim and raised pectoral fin have also been recorded as part of gray whale courtship behavior (Sauer, 1963).

The development of socio-sexual behavior in beluga calves is a process that begins within the first year of life. The frequency of socio-sexual behavior has been

found to increase steadily throughout the first three years of life and seems to become even more common throughout the juvenile years for the male belugas, though only the first three years of life have been assessed for frequency of socio-sexual interactions (Silva, 2017). The duration, but not frequency, of socio-sexual behavior bouts is longer when the receiver of the interaction is male, suggesting that social setting does affect socio-sexual behavior to some degree (Silva, 2017). These social interactions between belugas may be crucial for developing bonds with other individuals and for learning the necessary behaviors for successful mating behavior later in life.

Beluga Whale Social Learning, Play, and Social Bonds

Beluga whales may remain with their mothers for several years, relying heavily on milk as a form of nutrition in the first year of life (Matthews & Ferguson, 2015). Beluga calves stay relatively close by or trailing their mothers for the first year of life, which may serve as protection, but may also facilitate social learning as the calf learns how to behave in an ever-changing aquatic environment (Krasanova, Bel'kovich, & Chernetsky, 2006). In human care, beluga calves show behavioral trends consistent with wild observations, transitioning from time spent predominantly with their mother to spending more time interacting with other individuals or swimming on their own (Hill, 2009; Hill, Campbell, Dalton, & Osborn, 2013). Adult males have not been observed to provide allocare in the first year, although female and younger male conspecifics spend time interacting with the calf (Hill & Campbell, 2014).

Young belugas may learn new motor behaviors by imitating adult behavior (Krasanova, Bel'kovich, & Chernetsky, 2009), but this hypothesis needs much more investigation; however, beluga whales have demonstrated their ability to mimic on-

command motor actions that were demonstrated previously by a conspecific, as well as to produce vocalizations that mimic recordings of themselves, artificial sounds, and human-made sounds (Abramson et al., 2017; Murayama, Iijima, Katsumata, & Arai, 2014). Additionally, other cetaceans including bottlenose dolphins and killer whales show experimental evidence for the ability to copy another conspecific's behavior, which may allow for behaviors to be learned socially in both a wild and captive setting (Abramson, Hernandez-Lloreda, Call, & Colmenares, 2012; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Kuczaj & Yeater, 2006). Social learning has been reported in many different species of animals, though one review had suggested that sex differences in social learning were commonly ignored, not reported, or not possible to conduct due to experimental set-up (Choleris & Kavaliers, 1999). The small amount of research that does exist points to potential sex differences in social learning of spatial tasks, food preferences, and the transmission of novel behaviors. Choleris and Kavaliers (1999) emphasized the need for more research on sex differences in social learning.

In cetaceans, there is evidence that young animals learn through play (Kuczaj, Makecha et al., 2006). Young belugas play more frequently than adult belugas and the presence of young belugas is associated with an increase in adult belugas' play (Hill, Guarino, Crandall, Lenhart, & Dietrich, 2015; Hill & Ramirez, 2014). If play helps young animals practice behavior and form social relationships, it can be hypothesized that socio-sexual play behavior may also serve these functions in belugas. Eventually, this socio-sexual play may result in tertiary outcomes, including increased social status and reproductive success (Burghardt, 2014).

In bottlenose dolphins, affiliations and bonds are formed between males who perform synchronous behaviors and engage in socio-sexual interactions (Connor et al., 2006). The lack of research on male-male relationships in belugas makes it difficult to determine if the same bonds are formed via similar behaviors in beluga whales as they are in dolphins. Based on beluga preferences to have a male partner for socio-sexual behavior during the third year of life, it is plausible that male-male relationships grow stronger as belugas age (Silva, 2017), which is not unexpected from research with bottlenose dolphins. Bottlenose dolphins begin to develop a preference for spending more time with same sex conspecifics as they mature, and males spend more time socializing than females (Krzyszczak, Patterson, Stanton, & Mann, 2017). This pattern is similar to that observed for beluga social development during the first three years of life (Silva, 2017). Furthermore, sex differences in contact behavior between juvenile Atlantic spotted dolphins are hypothesized to help build and test strong bonds between males, while creating a larger network of associates for females (Kaplan & Connor, 2017). Adult male beluga pairs do display a high level of synchrony in underwater bubble production that is only surpassed by mother-calf pairs, which could be an indicator of strong male-male relationships in adult belugas (George & Noonan, 2015).

Upon reaching sexual maturity (approximately 8 to 13 years-old), males leave their matrilineal group to associate with other males (Colbeck et al., 2013; Robeck et al., 2005). However, because mating behavior of belugas has not been commonly observed in the wild, it is unclear if adult males, typically together in pairs or groups, behave similarly to male bottlenose dolphin alliances. The prevalence of male-male socio-sexual behavior in human care found by Hill, Dietrich, and colleagues (2015) suggests that this

behavior is quite common in belugas and further study of subjects in this setting will expand the current knowledge of socio-sexual development in beluga whales (Hill & Lackups, 2010).

Social Learning and Conservation

Beluga whales are commonly found in groups that range from a few individuals to large groups when belugas make seasonal migrations to breeding grounds where hundreds of animals may gather. One population of belugas makes Cook Inlet, Alaska their permanent home with limited migration around the region and is currently endangered and facing extinction (N.O.A.A., 2017). Young belugas may learn these migration routes over the first several years of their lives while remaining with their mother (Colbeck et al., 2013). Due to the process of young belugas learning the migration route to breeding grounds from their mothers, it is unlikely that the Cook Inlet population of belugas will recover by means of individuals from other populations changing breeding grounds. Genetic analysis of North Pacific beluga whales has found that most belugas return to population-specific summering and wintering grounds each year, extending the unlikelihood that belugas from other populations would be likely to migrate to the Cook Inlet population (O’Corry-Crowe et al., 2018). It has been proposed that toothed whales, including beluga whales, are not able to recover as well from overexploitation in comparison to their baleen counterparts because toothed whales’ survival and reproductive fitness is much more dependent on social learning, social structures, and the transfer of skills between generations (Wade, Reeves, & Mesnick, 2012). Hobbs, Wade, and Shelden (2015) discuss loss of social knowledge passed down through generations of belugas as one contributing factor as to why the Cook Inlet

population has not recovered in recent years. As a result, studying other environmental and behavioral factors, such as pollution, prey availability, and the development of socio-sexual behavior are necessary for understanding how the Cook Inlet population can be better managed to avoid extinction (Hobbs et al., 2015).

Purpose of Study

Given the importance of better understanding how the socio-sexual behavior of beluga whales develops, the present study aimed to examine factors influencing the prevalence of involvement in socio-sexual behavior during development and changes in the behaviors of the socio-sexual repertoire during years 4 through 10 of life. The hypotheses of the present study were that socio-sexual development would depend on many individual, environmental, and social factors.

The first hypothesis was that socio-sexual behaviors would increase with age, especially for males, given the previous research that juvenile and adult males were more frequent participants in socio-sexual interactions compared to younger belugas (Hill, Dietrich, et al., 2015). Additionally, the prevalence of socio-sexual behavior for females was hypothesized to be less frequent compared to males, due to the tendency for adult females tend to display less socio-sexual behaviors compared to adult males (Hill, Dietrich, et al., 2015; Silva, 2017).

The second hypothesis was that socio-sexual behaviors would be more frequent when male conspecifics of the same age or older age as compared to the subject were present. Previous research suggested that adult males frequently engaged in socio-sexual behavior with juveniles (Hill, Dietrich, et al., 2015).

It was also hypothesized that socio-sexual behavior would be more prevalent during breeding months, as some socio-sexual behavior in belugas has been found to vary across months of the year and correspond with breeding seasons of wild belugas (Glabicky et al., 2010).

The presence of environmental enrichment devices (EEDs) was hypothesized to decrease the prevalence of socio-sexual behavior because enrichment may foster other types of play behavior, serve as a distraction from conspecifics, and is typically considered positive reinforcement.

Finally, it was hypothesized that different behaviors of the socio-sexual repertoire would be used preferentially by different subjects and that these behaviors would increase or decrease throughout development. Specifically, males were expected to show a greater diversity in their behaviors and specific behaviors, such as pelvic thrusts, were expected to increase in frequency with age. Previous studies have found that belugas housed in different facilities shared similar repertoires with differences occurring between individuals in the frequency with which they engaged in certain socio-sexual behaviors (Hill, Dietrich, et al., 2015).

CHAPTER II - METHOD

Subjects

The subjects of this study were five beluga whales (*Delphinapterus leucas*) (three males, two females) all born at SeaWorld San Antonio (SWSA) between 2007 and 2013. Each subject was housed with several other individuals, including at least one immature beluga whale within a few years of the same age. Daily social groupings varied based on facility activities and staff decisions. Table 1 summarizes the subjects, their birth years, and dates of data collection for the present study.

Each subject spent the first several years of life at SWSA. After this time, two subjects were transferred to Georgia Aquarium (GA), one passed away, and two remained at SWSA. Data from the first three years of life were previously analyzed as part of another project. Consequently, the present study analyzed behavior starting in the fourth year of life and continued for as long data was available for each subject.

While at SWSA, subjects were housed in a series of seven connected pools that held approximately 2 million gallons of water. Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) were also housed within this facility, and usually occupied the pools, which were adjacent to the belugas at any given time. The belugas and Pacific white-sided dolphins sometimes interacted through gates or net walls. While at GA, subjects were housed in approximately 800,000 gallons of water among three interconnected pools along with a few other beluga whales and harbor seals (*Phoca vitulina*) within the same enclosure.

Table 1
Relevant Demographics and Available Data

Subject	Location	Birthdate	Data Start Date	Data End Date	Age Start	Age End	Sex
OLI	SWSA	6/23/2007	6/23/10	6/22/17	4	10	M
GRA	SWSA	6/26/2007	6/26/10	11/21/10	4	4	M
	GA		4/26/13	3/26/15	6	8	
QIN*	GA	7/31/2008	4/30/13	3/31/15	5	7	F
BEL	SWSA	6/12/2009	6/12/12	8/12/13	4	5	F
SAM	SWSA	7/9/2013	7/9/16	7/9/17	4	4	M

Note. *born at SWSA, transferred to GA 2010.

Data Collection

Data were collected via video recordings from 2007 to 2017 at SWSA and from 2013 to 2015 at GA. Videos were a combination of both scan samples and focal follows. Scan sample videos typically lasted 20 minutes and attempted to capture the behavior of several individuals at one-minute intervals, while focal follow videos lasted 15 minutes in length and followed the behavior of one individual, whenever visible, for the entirety of the video.

For the present study, four videos per month for each individual subject were selected randomly for coding. Focal follows were used whenever possible; however, as the animals increased in age, fewer focal follow videos were taken, making it necessary to use the scan sample videos. Video recordings were taken between 0600 and 1800 when trainers were absent, and the sample included recordings spread across the day. In total, the data set for the present study consisted of 587 videos, which represented 157 hours.

Video Analysis

Videos were coded for the measures and behaviors listed in Appendix A, which also contains operational definitions of these behaviors. The initiator and recipient of each socio-sexual interaction were also noted. Additionally, all non-sexual social interactions were coded, including affiliative and agonistic interactions. Information was also recorded for each video regarding the presence/absence of environmental enrichment devices (EEDs), age of subject, and identity of all other subjects present in the same enclosure. Sex and age class of other individuals were coded as Adult (over 11-years-old), Sub-adult (7- to 10-years old), Juvenile (weaned but 4- to 6-years-old), and Calf (birth to 3-years-old).

Two people were trained to code the videos using the same methods of previous studies (Hill, Dietrich, et al., 2015; Silva, 2017). Reliability was assessed on 10% of the present dataset and found to be at least 80% for each of the variables coded in this study.

Statistical Analysis

Due to differences in the number and type of video recordings available for each subject, the duration of all behaviors was calculated as a proportion of the time the subject was visible in the recordings. In order to determine how often certain behaviors were used as part of the socio-sexual repertoire, the frequency of each behavior was divided by the number of clearly visible interactions initiated by the subject. Several of these variables were found to have a positively or negatively skewed distribution and thus were log transformed before statistical analyses were performed (Field, 2013).

To test the effects of several variables on the occurrence of socio-sexual behavior, a logistic regression was performed and included the predictor variables of age of subject,

sex of subject, sex and age of enclosure mates, month of the year, and presence of EEDs. Activity budgets were created for each year of life for a comparison to the subjects' behavior across years and between individuals. Finally, in order to assess how the specific behaviors that comprise the socio-sexual repertoire change through development and vary between individuals, a series of MANOVAs were performed.

The comparisons between individuals and across years were made through several different comparisons. OLI, GRA, BEL, and SAM's data from the fourth year of life were compared to look at differences between individuals and previously reported results from the third year of life. Further comparisons were made across years four through ten of OLI's life, as the dataset contains continuous and consistent data across all OLI's years of life and thus can be used to look at developmental patterns. Finally, OLI and GRA were directly compared to one another, as they were both males who spent the first four years of life in the same facility and were then housed at separate facilities, experiencing different social groupings. Data from years four, seven, and eight of OLI and GRA's life were compared in order to assess any between or within subject differences in prevalence or repertoire of socio-sexual behavior.

CHAPTER III - RESULTS

Factors Influencing the Occurrence of Socio-sexual Behavior

A binary logistic regression model was tested to determine the relationship of several factors with the subjects' involvement in socio-sexual behavior. The model predicted the subjects' involvement in socio-sexual behavior using the predictor variables of subject age in years, sex of subject, month of year, presence of EEDs, and age and sex of enclosure mates was significant, $\chi^2(22) = 131.72, p < .001$, (Table 2). This model correctly classified 72.4% of cases and was an improvement over the naïve model, which correctly classified 61.6% of cases. The odds ratios of the significant predictor variables indicated that the odds of the subject engaging in socio-sexual behavior were 1.22 times more likely in the fifth year of life compared to the fourth year of life, 2.44 times more likely for male subjects compared to female subjects, 2.49 times more likely if a sub-adult male conspecific was present compared to when one was not, 1.93 times more likely when a juvenile male was present compared to when one was not, and 6.52 times more likely when a male calf was present compared to when one was not. Finally, the odds of the subject engaging in socio-sexual behavior were 2.92 times more likely in February compared to January and 4.62 times more likely in May compared to January.

A second binary logistic regression model was tested to determine the relationship of several factors with the initiation of socio-sexual behavior by the study's subjects. The model predicted the subjects' initiation of socio-sexual behavior using the predictor variables of subject age in years, sex of subject, month of year, presence of EEDs, and age and sex of enclosure mates as predictor variables $\chi^2(22) = 158.04, p < .001$, (Table 3). This model correctly classified 79.0% of cases and was an improvement over the naïve

model, which correctly classified 70.8% of cases. The odds ratios of significant predictor variables indicated that the odds of the subject initiating socio-sexual behavior were 3.88 times more likely for male subjects compared to female subjects, 8.01 times more likely when a male calf was present compared to when one was not, and 3.63 times more likely in May compared to January.

Table 2
Coefficients of the Model Predicting the Involvement of the Subject in Socio-sexual Behavior

Factors	Exp (B)	95% CI for Exp (B)		Significance
		Lower	Upper	
Constant	0.05			
Year of Life	1.22	1.06	1.41	.007*
Male Subject	2.44	1.27	4.72	.007*
EED Present	0.78	0.51	1.20	.265
Adult Male Present	1.13	0.70	1.82	.619
Adult Female Present	3.80	0.26	56.71	.332
Sub-adult Male Present	2.49	1.16	5.36	.020*
Sub-adult Female Present	1.67	0.83	3.35	.148
Juvenile Male Present	1.93	1.03	3.62	.042*
Juvenile Female Present	1.30	0.77	2.18	.327
Calf Male Present	6.52	3.54	12.02	<.001*
Calf Female Present	1.40	0.84	2.34	.202
February	2.92	1.08	7.91	.035*
March	1.10	0.40	3.04	.853
April	2.19	0.74	6.49	.158
May	4.62	1.67	12.77	.003*
June	2.19	0.81	5.95	.125
July	1.65	0.63	4.35	.308
August	1.44	0.54	3.83	.463
September	1.60	0.61	4.23	.344
October	1.73	0.67	4.49	.260
November	1.99	0.76	5.18	.159
December	1.32	0.48	3.63	.596

Note. * $p < 0.05$.

Table 3
Coefficients of the Model Predicting the Subjects' Initiation of Socio-sexual Behavior

Factors	Exp (B)	95% CI for Exp (B)		Significance
		Lower	Upper	
Constant	0.07			
Year of Life	1.14	0.96	1.35	.129
Male Subject	3.88	1.66	9.09	.002*
EED Present	0.74	0.45	1.20	.215
Adult Male Present	1.61	0.93	2.80	.089
Adult Female Present	1.88	0.13	27.45	.645
Sub-adult Male Present	0.94	0.38	2.35	.890
Sub-adult Female Present	1.37	0.64	2.95	.415
Juvenile Male Present	1.79	0.92	3.52	.089
Juvenile Female Present	1.37	0.78	2.40	.274
Calf Male Present	8.01	4.35	14.76	<.001*
Calf Female Present	1.26	0.73	2.17	.401
February	1.51	0.50	4.62	.466
March	1.05	0.34	3.25	.932
April	0.77	0.23	2.61	.672
May	3.63	1.21	10.88	.021*
June	1.38	0.45	4.21	.575
July	2.57	0.91	7.28	.075
August	1.75	0.60	5.10	.308
September	1.71	0.58	5.01	.328
October	1.37	0.47	3.99	.566
November	1.23	0.41	3.70	.707
December	1.07	0.34	3.38	.908

Note. * $p < 0.05$.

Activity Budgets

Fourth Year of Life

Collapsing data across all five subjects found that in the fourth year of life, 3.20% of time was spent involved in socio-sexual interactions, though interactions initiated by the 4-year-old focal subjects totaled 0.63% of their time. Subjects' individual activity budgets varied in how much time was spent in socio-sexual, agonistic, and affiliative

interactions, despite solo swims comprising the majority of time for all subjects in the fourth year of life (See Figure 1). On average, subjects were involved in 13.22 socio-sexual interactions per hour and initiated 3.10 socio-sexual interactions per hour. There was a significant difference between subjects in the amount of time were involved in socio-sexual behavior, $F(3, 50.68) = 9.07, p < .001, \hat{\omega}_p^2 = .31$. Post hoc analyses with a Games- Howell comparison found that SAM spent significantly more time involved in socio-sexual behavior compared to OLI, GRA, and BEL ($p < .001, p = .001, p = .004$), but no other comparisons were statistically significant. There was also a significant main effect of individual on the time spent in socio-sexual interactions that the subject initiated, $F(3, 50.89) = 4.68, p = .006, \hat{\omega}_p^2 = .17$, with SAM initiating socio-sexual interactions that totaled significantly more time compared to OLI ($p < .001$).

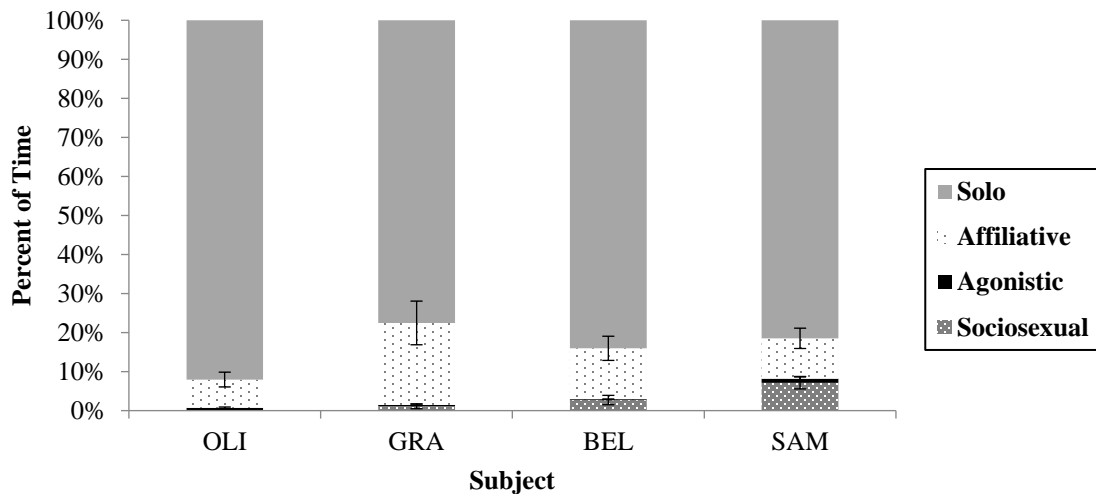


Figure 1. Activity budgets for the fourth year of life across subjects. Error bars represent SEM.

In comparison, there was no significant difference between subjects in the amount of time spent in agonistic interactions, $F(3, 57.37) = 1.81, p = .154, \hat{\omega}_p^2 = .04$; however,

there was a significant main effect of subject in the amount of time spent in affiliative interactions, $F(3, 147) = 2.75, p = .045, \eta^2 = .06$. Post hoc analyses with a Bonferroni comparison revealed that GRA spent significantly more time in affiliative interactions compared to OLI ($p < .037$), but that no other comparisons were significant.

Longitudinal Single Case

Activity budgets across years four through ten of OLI's life are presented in Figure 2 and show that while solo swimming comprised the majority of his time across all years, the amount of time OLI was involved in socio-sexual interactions generally increased through development. There was a significant main effect of year on time spent in socio-sexual interactions, $F(6, 110.12) = 19.06, p < .001, \hat{\omega}_p^2 = .48$, with Games-Howell post hoc analyses indicating that significantly more socio-sexual behavior occurred during years 8 and 9 compared to years 4, 5, 6, and 7. The amount of time OLI spent in socio-sexual interactions that he initiated also changed across the years, $F(6, 109.56) = 14.97, p < .001, \hat{\omega}_p^2 = .42$, with more time spent in events initiated by OLI in years 8 and 9 compared to several of the previous years. See Table 4 for all comparisons. The amount of time OLI spent in interactions he initiated was about 50% of the total time he spent in all socio-sexual interactions (See Figure 3). A significant difference in affiliative interactions was also found, $F(6, 122.76) = 2.5, p = .026, \hat{\omega}_p^2 = .06$, with a Games-Howell post hoc indicating approaching significance for OLI being involved in less social interactions during year 5 compared to year 8 ($p = .054$) and year 9 ($p = .068$). There were no significant differences across years in the time spent in agonistic interactions, $F(6, 288) = 0.43, p = .858, \eta^2 = .00$.

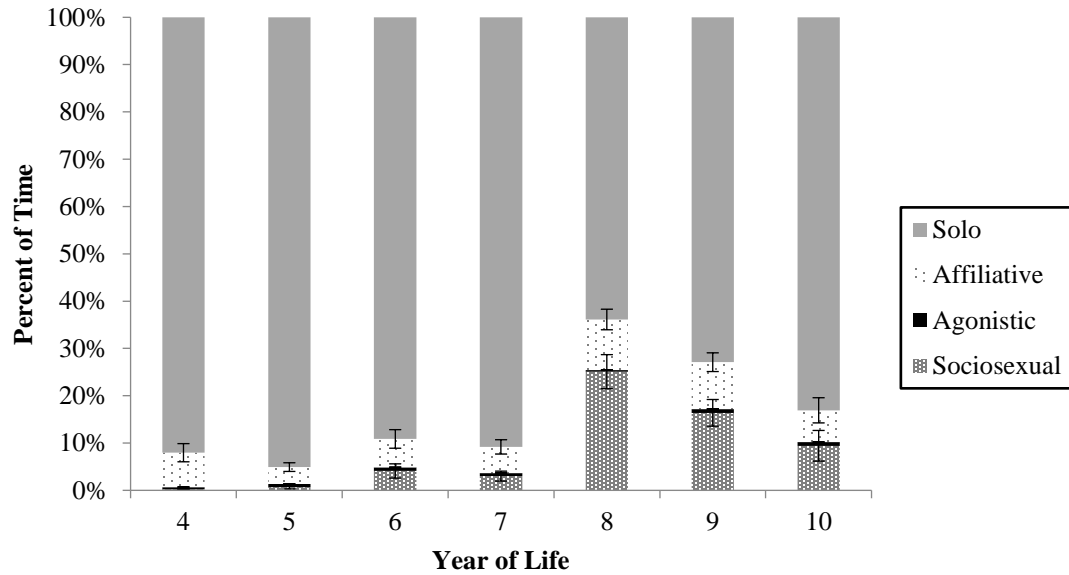


Figure 2. Activity budgets for OLI across years of life.
Error bars represent SEM.

Table 4
Comparisons of OLI's Duration Involved and Initiated Socio-sexual Behavior Across Years of Life

Comparison of OLI's Duration of Involved Socio-sexual Behavior for Years Four through Ten			
Year	Year	Difference ¹	Significance
4	5	-0.002	0.866
4	6	-0.015	0.127
4	7	-0.011	0.124
4	8	-0.089	<.001*
4	9	-0.060	<.001*
4	10	-0.033	0.062
5	6	-0.013	0.274
5	7	-0.009	0.354
5	8	-0.087	<.001*
5	9	-0.058	<.001*
5	10	-0.032	0.095
6	7	0.004	0.998
6	8	-0.073	<.001*
6	9	-0.045	0.004*
6	10	-0.018	0.754
7	8	-0.077	<.001*
7	9	-0.049	0.001*
7	10	-0.022	0.498
8	9	0.028	0.530
8	10	0.055	0.015
9	10	0.027	0.547

Table 4 Continued

Comparison of OLI's Duration of Initiated Socio-sexual Behavior for Years Four through Ten			
Year	Year	Difference ¹	Significance
4	5	-0.001	0.714
4	6	-0.009	0.191
4	7	-0.005	0.515
4	8	-0.058	<.001*
4	9	-0.034	<.001*
4	10	-0.021	0.033*
5	6	-0.008	0.294
5	7	-0.004	0.742
5	8	-0.057	<.001*
5	9	-0.033	<.001*
5	10	-0.02	0.045*
6	7	0.005	0.946
6	8	-0.046	<.001*
6	9	-0.025	0.018*
6	10	-0.01	0.661
7	8	-0.053	<.001*
7	9	-0.029	0.001*
7	10	-0.017	0.215
8	9	-0.024	0.332
8	10	0.013	0.781
9	10	-0.012	0.781

Note. ¹ is difference of values log-transformed; **p* < .05

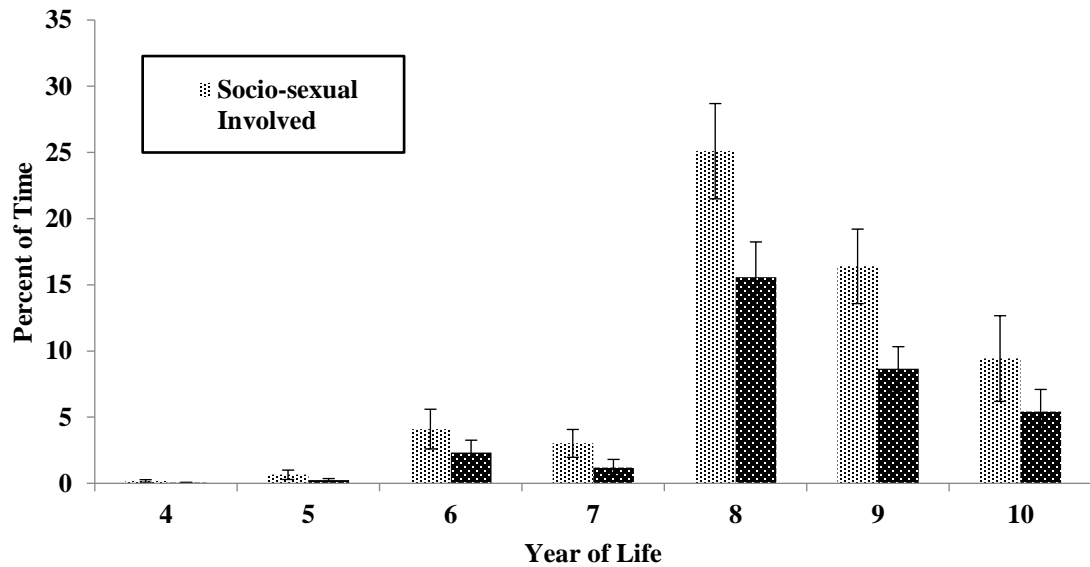


Figure 3. Comparison of OLI's involvement in and initiation of socio-sexual behavior across years of life.

Number of conspecifics (Mature Males: Mature Females: Immature Males: Immature Females) during each year of life were: Year 4 (0:4:1:3), Year 5 (1:4:0:2), Year 6 (1:4:1:2), Year 7 (1:4:1:1), Year 8 (1:4:1:1), Year 9 (1:4:1:0), and Year 10 (1:4:2:0). Error bars represent SEM.

Comparison of Sub-adult Males

Data from years 4, 7, and 8 were compared for OLI and GRA, who were housed at the same facility in year 4 but at separate facilities in years 7 and 8. Activity budgets are displayed in Figure 4, and show that the majority of the time for both subjects was spent solo swimming, affiliative and socio-sexual behavior varied throughout the years, and agonistic behavior comprised very little of the subjects' time. A Greenhouse-Geisser test was used to determine that there was a significant interaction between year of life and subject in the proportion of time spent involved in socio-sexual behavior, $F(1.08, 40.10) = 13.76, p < .001, \eta^2 = .271$. There was also a significant main effect of year on time spent in socio-sexual behavior, $F(1.08, 40.10) = 15.14, p < .001, \eta^2 = 0.29$ and a significant difference between subjects on time spent in socio-sexual behavior, $F(1, 37) = 15.68, p < .001, \eta^2 = .298$. Overall, OLI spent more time involved in socio-sexual behavior, but when comparing across years of life, post-hoc analyses revealed that significantly more time was spent in socio-sexual behavior in year 8 compared to year 7 and year 4 ($p < .001$), but that years 4 and 7 were not different from each other ($p = 1.00$). Additionally, a significant interaction of year and subject on the percent of time spent in affiliative behavior was revealed, $F(1.59, 58.96) = 9.93, p < .001, \eta^2 = .212$. There were also main effects of year, $F(1.59, 58.96) = 5.80, p = .008, \eta^2 = .136$ and subject $F(1, 37) = 4.31, p = .045, \eta^2 = .104$, on the percent of time spend in affiliative behavior, with OLI significantly more involved in affiliative interactions compared to GRA, and year 8 had significantly less affiliative behavior compared to year four ($p = .020$). In contrast, a Greenhouse-Geisser test revealed that there were no interactions of subject and year on the percent of time spend in agonistic interactions, $F(1.35, 49.42) = 0.46, p = .558, \eta^2 =$

.012, nor were there main effects of subject $F(1, 37) = 2.69, p = .109, \eta^2 = 0.068$, or year $F(1.34, 49.42) = 2.83, p = .088, \eta^2 = .071$.

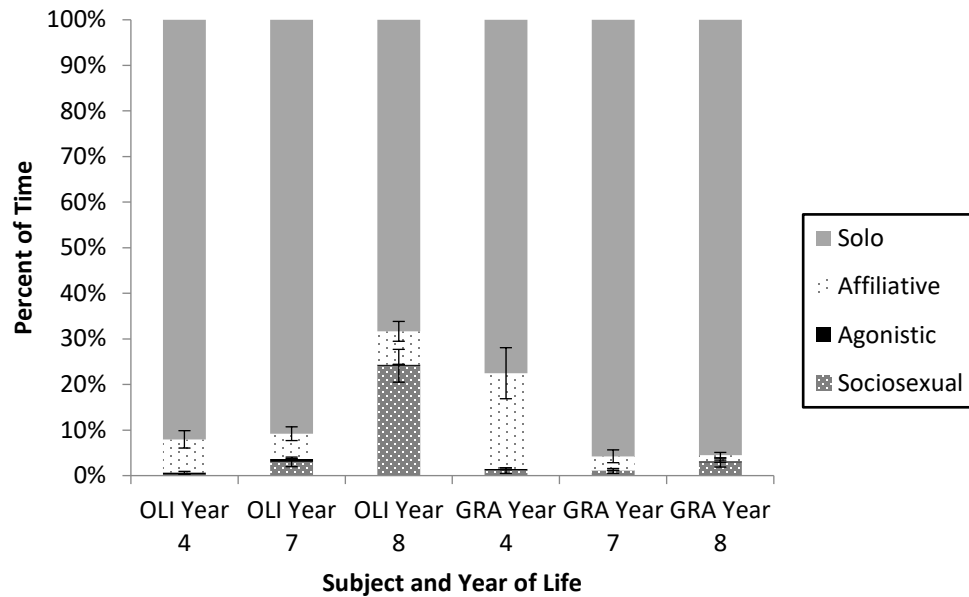


Figure 4. Activity budgets for OLI and GRA during years four, seven, and eight of life. Error bars represent SEM.

Use of the Socio-sexual Repertoire

Fourth Year of Life

During the fourth year of life, subjects frequently exhibited several behaviors when engaged in socio-sexual behavior (See Figure 5). For interactions initiated by the subject, the most commonly displayed behaviors across all four individuals were lateral swims (79% of interactions), pectoral fin up (77% of interactions), and side presented (76% of interactions). Open mouths, horizontal s-postures, genital rubs, thrusts, and bubbles were sometimes exhibited, but not in the majority of interactions. Despite individual variation, there were no statistically significant differences between individual subjects in how often specific behaviors were displayed in socio-sexual interactions.

Descriptively, BEL performed more genital rubs and fewer thrusts, bubbles, and horizontal s-postures compared to the other subjects during the fourth year of life.

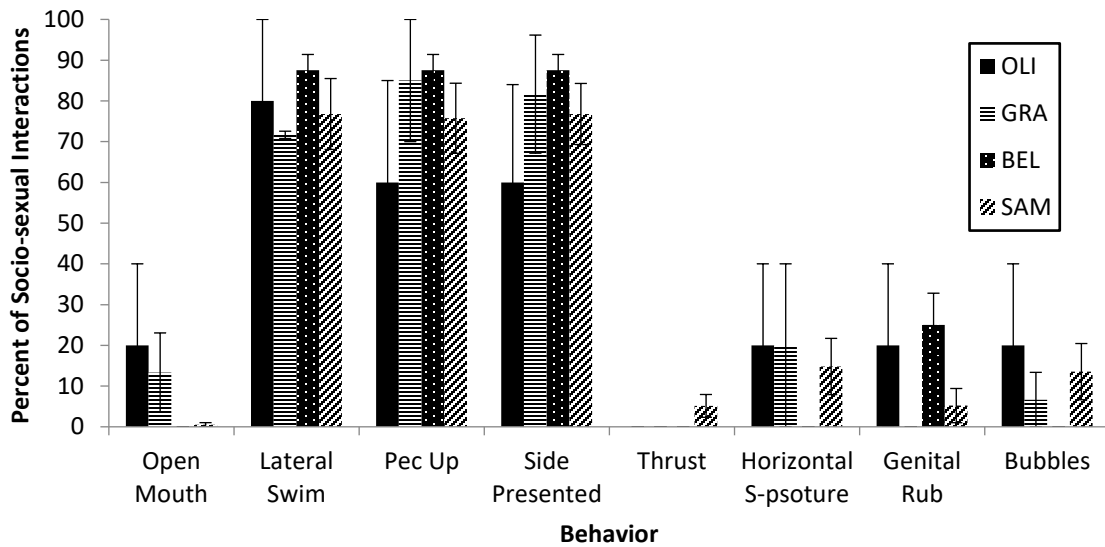


Figure 5. Behaviors performed during the fourth year of life across individuals. Error bars represent SEM.

Longitudinal Single Case

Comparing the use of different behaviors across years 4 through 10 of OLI’s life revealed that some behaviors, including lateral swims, pectoral fin up, and side presentations, were displayed frequently while engaged in socio-sexual behavior, but the frequency of these behaviors did not change across years (Figure 6). Other behaviors, including open mouths, erections, vertical s-postures, and bubbles were displayed relatively infrequently, though consistently, across years (Figure 6). The behaviors with a significant difference in frequency across years included genital rubs, thrusts, and horizontal s-postures (Figure 7). The frequency of genital rubs generally decreased across years with an overall significant difference between years, $F(6, 24.37) = 6.50, p < .001, \hat{\omega}_p^2 = .51$. Games-Howell post-hoc analysis revealed that there were significantly fewer

genital rubs in year 10 compared to year 6 ($p = .030$) and year 8 ($p = .001$). In contrast, the frequency of horizontal s-postures, $F(6, 111) = 3.32, p = .005, \eta^2 = .180$, and thrusts, $F(6, 111) = 3.12, p = .007, \eta^2 = .169$, were found to significantly differ across the years of life, with a general increase in frequency across years. Specifically, the frequency of horizontal s-postures was greater in year 8 compared to year five ($p = .026$), and the frequency of thrusts was less in year 4 compared to years 8 ($p < .001$), 9 ($p < .001$), and 10 ($p = .002$), and less in year five compared to years 8 ($p < .001$), 9 ($p = .019$), and 10 ($p = .012$).

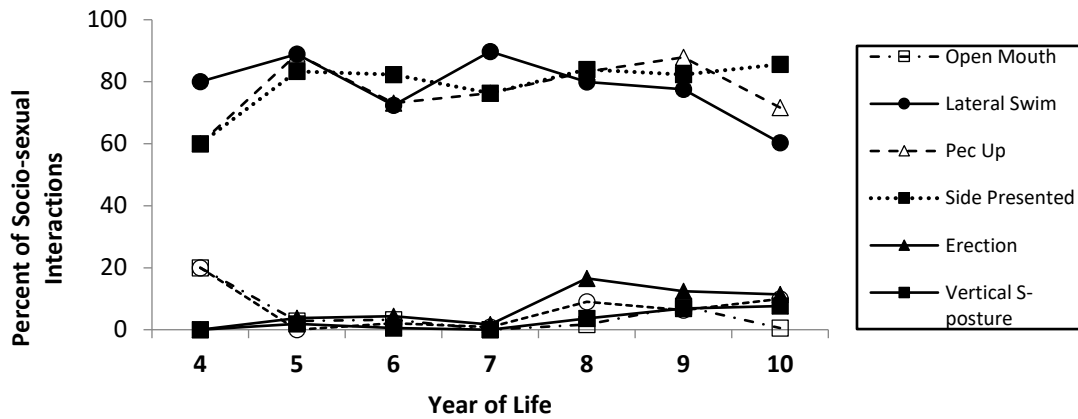


Figure 6. Behaviors of the socio-sexual repertoire that did not change in usage across development.

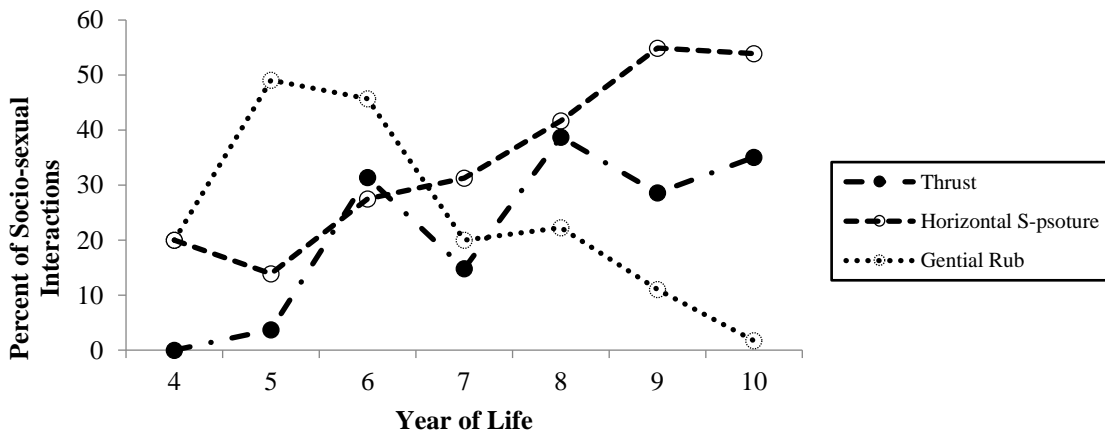


Figure 7. Behaviors of the socio-sexual repertoire that changed in usage across development.

Comparison of Sub-adult Males

Mixed ANOVAs comparing the frequency of specific socio-sexual behaviors during years 4, 7, and 8 for OLI and GRA found several differences between subjects and across years of life (Table 5). Some behaviors, including lateral swims, pectoral fin up, and side presentations were quite frequent across years for both subjects, while other behaviors, including erections and thrusts, were quite infrequent, only present in years 7 and 8, and were predominately performed by OLI (Figure 8).

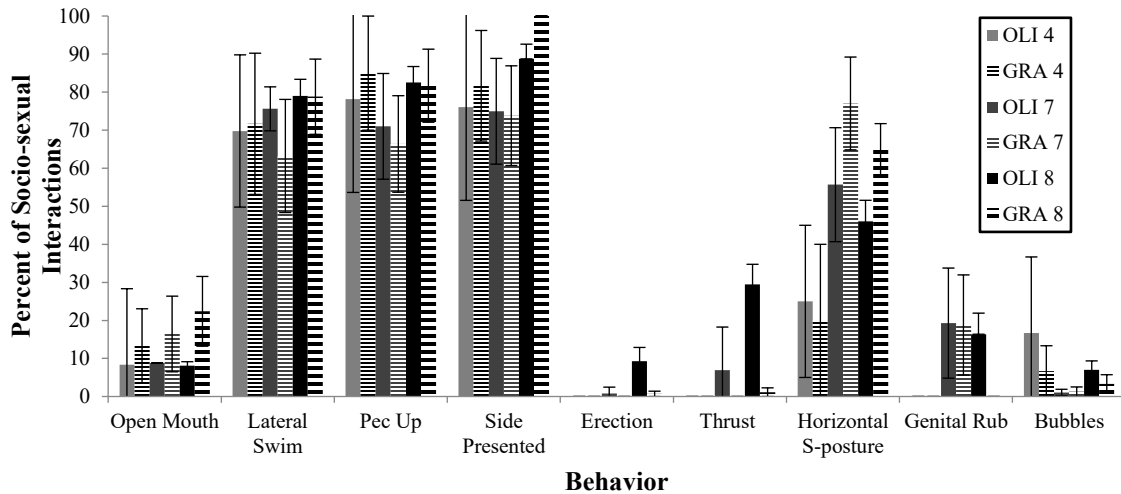


Figure 8. Behaviors performed by OLI and GRA during years 4, 7, and 8 of life.

Table 5
Comparing Behaviors of OLI and GRA Across Years 4, 7, and 8 of Life

Behavior	Comparison	Test	Effect Size	Significant Post-hoc
Open Mouth	Year of Life x Subject	$F(1.6, 145.5) = .29$, $p = .706$	$\eta^2 = .003$	
	Year of Life	$F(1.6, 145.5) = 2.19$, $p = .125$	$\eta^2 = .024$	
	Subject	$F(1, 89) = 4.77$, $p = .032^*$	$\eta^2 = .051$	OLI < GRA
Lateral Swim	Year of Life x Subject	$F(1.90, 169.40) = 6.45$, $p = .002^*$	$\eta^2 = .068$	
	Year of Life	$F(1.90, 169.40) = 17.03$, $p < .001^*$	$\eta^2 = .161$	Year 8 > Year 4 ($p < .001$); Year 8 > Year 7 ($p = .001$)
	Subject	$F(1, 89) = 7.69$, $p = .007^*$	$\eta^2 = .079$	OLI > GRA
Pectoral Fin Up	Year of Life x Subject	$F(1.88, 167.00) = 7.62$, $p = .001^*$	$\eta^2 = .079$	
	Year of Life	$F(1.88, 167.00) = 17.79$, $p < .001^*$	$\eta^2 = .167$	Year 8 > Year 4 ($p < .001$); Year 8 > Year 7 ($p < .001$)
	Subject	$F(1, 89) = 7.08$, $p = .009^*$	$\eta^2 = .074$	OLI > GRA
Side Presented	Year of Life x Subject	$F(1.83, 163.19) = 5.54$, $p = .006^*$	$\eta^2 = .059$	
	Year of Life	$F(1.83, 163.19) = 19.76$, $p < .001^*$	$\eta^2 = .182$	
	Subject	$F(1, 89) = 4.51$, $p = .036^*$	$\eta^2 = .048$	OLI > GRA
Erection	Year of Life x Subject	$F(1.02, 91.15) = 13.06$, $p < .001^*$	$\eta^2 = .128$	
	Year of Life	$F(1.02, 91.15) = 14.32$, $p < .001^*$	$\eta^2 = .139$	Year 8 > Year 4 ($p = .001$); Year 8 > Year 7 ($p = .001$)
	Subject	$F(1, 89) = 12.52$, $p = .001^*$	$\eta^2 = .123$	OLI > GRA
Thrust	Year of Life x Subject	$F(1.21, 108.04) = 28.39$, $p < .001^*$	$\eta^2 = .242$	
	Year of Life	$F(1.21, 108.04) = 29.85$, $p < .001^*$	$\eta^2 = .251$	Year 8 > Year 4 ($p < .001$); Year 8 > Year 7 ($p < .001$)
	Subject	$F(1, 89) = 40.55$, $p < .001^*$	$\eta^2 = .313$	
Horizontal S-posture	Year of Life x Subject	$F(1.91, 170.03) = 2.39$, $p = .097$	$\eta^2 = .026$	
	Year of Life	$F(1.91, 170.03) = 9.35$, $p < .001^*$	$\eta^2 = .095$	Year 8 > Year 4 ($p < .001$)
	Subject	$F(1, 89) = 0.001$, $p = .975$	$\eta^2 = .000$	
Genital Rub	Year of Life x Subject	$F(1.68, 149.42) = 9.97$, $p < .001^*$	$\eta^2 = .101$	
	Year of Life	$F(1.68, 149.42) = 7.63$, $p = .001^*$	$\eta^2 = .079$	Year 8 > Year 4 ($p < .001$)
	Subject	$F(1, 89) = 8.72$, $p = .004^*$	$\eta^2 = .09$	OLI > GRA
Bubbles	Year of Life x Subject	$F(1.55, 137.88) = 2.81$, $p = .077$	$\eta^2 = .031$	
	Year of Life	$F(1.55, 137.88) = 4.08$, $p = .028^*$	$\eta^2 = .044$	Year 8 > Year 7 ($p = .002$)
	Subject	$F(1, 89) = 5.78$, $p = .018^*$	$\eta^2 = .061$	OLI > GRA

CHAPTER IV – DISCUSSION

Developmental Factors Influencing Socio-sexual Behavior

From previous research, it is clear that beluga whales participate in socio-sexual behavior from a young age (Hill, Dietrich, et al., 2015). A developmental perspective on the changes in frequency of socio-sexual behavior and when the specific behaviors of the socio-sexual repertoire appear has not been previously reported in the literature.

Consequently, this study examined the socio-sexual development in belugas starting in the fourth year of life. Research on the behavioral development of other cetacean species suggests that complex behaviors are learned over time and likely develop from practice with conspecifics (Kuczaj & Yeater, 2006).

Based on the report of Silva (2017), belugas in their third year of life spent an average of 0.33% of time in socio-sexual interactions that they initiated. The current study reveals that in the fourth year of life this amount of time almost doubled to 0.63% of time or approximately 9 minutes per day. Time spent in subject-initiated interactions was a relatively small portion of time compared to the total of 3.20% of time, 46 minutes per day, that belugas were involved in socio-sexual interactions during their fourth year of life. As displayed in Figure 1, all subjects in the present study spent a majority of time, about 80-90% during the fourth year of life in solo swims, about 10-20% of time in affiliative interactions, and smaller portions of time in agonistic and socio-sexual interactions.

The activity budgets of OLI's fourth to tenth years of life indicate that the amount of time he was involved in affiliative and agonistic interactions did not significantly

change through development. In contrast, there was a significant increase in socio-sexual behavior involvement and initiation as OLI matured. Given the previous research that adult male belugas frequently engage in socio-sexual behavior with other adult males (Glabicky et al., 2010), it is not surprising that OLI spent more time engaged in socio-sexual behavior as he approached maturity and initiated more of these interactions, as well. The increase in socio-sexual behavior may be explained by a need to practice socio-sexual behavior before reaching maturity and/or by a need to form social bonds with other male conspecifics, as has been suggested for bottlenose dolphins (Harvey et al., 2017). Recent research suggests that male-male bonding is a more likely explanation, as sex-specific affiliation patterns emerge within the first five years of belugas' lives (Mazikowski, Hill, & Noonan, 2018). Further research regarding the partners of each socio-sexual interaction could help determine which of these factors are likely to explain this increase.

Data analysis conducted as part of the present study suggested, as hypothesized, that age is a good predictor of the likelihood of involvement in socio-sexual behavior, with odds of socio-sexual behavior occurring 1.22 times more likely in any given year compared to the previous year for years 4 through 10. Contrary to hypotheses, age was not a significant predictor of initiation of socio-sexual behavior. This finding may be due to the nature of binary logistic regression, which does not account for how many times an individual initiated. Instead, this analysis only accounts for the presence or absence of initiation in a particular scenario. It is likely that the act of initiating, rather than being involved, may depend more on the availability of social partners or month of year than on age.

One hypothesis of the present study suggested that the use of specific behaviors in the socio-sexual repertoire would change over the course of development. Hill, Dietrich, and colleagues (2015) presented several different behaviors that were part of the socio-sexual repertoire. Supporting the hypothesis, some behaviors of the repertoire were exhibited more than others and the prevalence of some behaviors changed throughout development. Though there were no significant differences between individuals in which behaviors were displayed during the fourth year of life, it did appear that some behaviors, such as erections, horizontal s-postures, and thrusts only appeared later in development. Lateral swims, pectoral fins up, and side presentations were the most frequently displayed behaviors throughout years 4 through 10. Behaviors that significantly increased in later years were horizontal s-postures and thrusts while genital rubs decreased.

If beluga whales need to practice specific behaviors before they are mature in order to be reproductively successful, this would explain why the behaviors more critical to mating, such as positioning the pelvic region correctly and thrusting in the correct direction, develop over time and with practice. Despite the frequency of erections not changing significantly across years, for OLI there is a substantial descriptive increase in erection frequency from earlier years to years 8, 9, and 10 of life. The frequency of open mouths during socio-sexual interactions also increased descriptively, though not significantly, during the later years of the study, while the other behaviors of the socio-sexual repertoire did not change substantially across development.

Social Factors Influencing Socio-sexual Behavior

Though there were variations between individuals during the fourth year of life, only SAM spent significantly more time involved in socio-sexual behavior compared to

the other subjects. There were no significant differences between individuals in the amount of time spent in agonistic interactions during the fourth year of life and only GRA spent more time in affiliative interactions compared to OLI. Although OLI and GRA experienced similar social conditions during the fourth year of life, GRA was housed with his mother during this time and often pair swam with her, while OLI was not housed with his mother. Additionally, SAM's mother was occupied with her subsequent calf during his fourth year, and BEL's mother was pregnant again during BEL's fourth year of life. Thus, GRA's increased amount of time spent in affiliative behavior may be explained by the availability of his mother.

Despite comparisons of female to male subjects during the fourth year of life failing to reveal sex differences in that BEL was not significantly different in her activity budgets or socio-sexual repertoire compared to the male subjects, the binary logistic regression model suggested that subject sex was a significant predictor of whether an individual would be involved in and also initiate socio-sexual behavior. The odds of a subject being involved in socio-sexual behavior were 2.44 times more likely for male compared to female subjects and the odds of a subject initiating socio-sexual behavior were 3.88 times more likely for male compared to female subjects. Unfortunately, the dataset did not contain any videos of females in their sub-adult years and there was not sufficient overlap in age between males and female in late juvenile years for a valid statistical comparison to test the hypothesis that females gradually reduce their socio-sexual interactions as they reach maturity. Previous research indicates that adult females engage in very few socio-sexual interactions and almost always swim solo when not with a dependent calf (Hill et al., 2018). This is in contrast to adult males that frequently

socialize with other adult males and continue to engage in socio-sexual behavior frequently during adulthood (Glabicky et al., 2010; Hill et al., 2018). The only evidence from the present study of females engaging less in socio-sexual behavior, is that during year six of life QIN engaged in socio-sexual behavior only 0.3 % of her time, compared to OLI's 4.1 % during year six of life. However, this is not a completely telling comparison because OLI and QIN were living in different facilities with different social groupings during the sixth year of life, thereby limiting the valid conclusions.

Sex differences in the behavioral repertoire are also difficult to test, as evidenced by no statistical differences between their sexes during the fourth year of life in the current study. Of course, females cannot have an erection and it would not make sense for the same thrusting motion to be as valuable to reproduction for them due to the need for the male to approach the female from a slightly posterior position for intromission to be successful. In contrast, behaviors such as side presentations and horizontal s-postures could be useful for females to practice for successful reproduction later in life, although not necessary for intromission. In the present study, BEL, a female, engaged in descriptively more genital rubs and fewer horizontal s-postures and thrusts compared to the male subjects. Although this trend is consistent with anticipated sex differences, further data collection of female belugas' behavior would help to resolve the question of when sex differences in repertoire become apparent during the developmental process.

Given that OLI initiated approximately half of the socio-sexual interactions in which he was involved, a ratio somewhat consistent across the years of his life, the other half of socio-sexual interactions were initiated by a conspecific or were unclear as to which animal was the initiator. The large proportion of interactions initiated by another

individual demonstrates the importance and necessity of conspecifics for initiating interactions.

Although it is still possible that an adult male may be necessary for demonstrating socio-sexual behaviors, the present study suggests that the immediate presence of an adult male is not a significant factor that increases the likelihood that socio-sexual behavior will occur. One hypothesis of the present study, that socio-sexual behavior would be more likely to occur when a male of the same or older age group was present, was only partially supported by the logistic regression analyses. In the prediction of both involvement in and initiation of socio-sexual behavior, the presence of a male calf greatly increased the odds of socio-sexual behavior by 6.52 and 8.01 times, respectively. Furthermore, the presence of a sub-adult male and juvenile male conspecific also significantly increased the odds that the subject would be involved in socio-sexual behavior. This finding is consistent with the behavior of wild bottlenose dolphins in that male calves are the most common actors and recipients of socio-sexual behavior (Mann, 2006).

The influence of young males' presence suggests that socio-sexual behavior possibly functions to provide bonding and practice opportunities for other males. Adult males often engage with other males for social interactions while females swim solo more often (Glabicky et al., 2010). Young belugas also demonstrate this sex-specific pattern of affiliation (Mazikowski et al., 2018), so it fits with past literature that younger male belugas also tend to engage in socio-sexual behavior with males as well. The strong influence of male calves in particular could be due to cultural traditions of males passing down the socio-sexual repertoire to younger males and potentially a tendency of male

calves to reciprocate in interactions. It has been suggested that many species of cetaceans pass down specific behaviors and traditions, forming what some consider to be culture (Rendell & Whitehead, 2001). The predictable and social nature of beluga migrations are suggested to be one aspect of culture in this species (O’Corry-Crowe et al., 2018).

Although adult male belugas have been previously reported to frequently engage in socio-sexual interactions, the present study suggests that adults do not significantly increase the prevalence of socio-sexual behavior for developing individuals in a social group where other young conspecifics are present. Despite this apparent lack of influence from adult males, a competing explanation might be that occasional interactions with adult males provide examples of socio-sexual behavior, but when grouped with younger individuals, a young beluga will seek out social partners closer in age. Mazikowski and colleagues (2018) found that young male belugas spend more time with young males than they do with belugas of other age-sex categories. Additionally, bottlenose dolphin calves were more likely to imitate behaviors of other calves compared to behaviors of adults (Kuczaj, Makecha et al., 2006). Overall prevalence of interactions aside, adult males may be necessary for young belugas to reach a threshold of exposure to developed socio-sexual behavior that is required for them to learn the full repertoire. Further research examining behavioral development in the complete absence of adult male role models would be necessary to test this prediction.

The comparison of GRA and OLI during years 4, 7, and 8 of their lives was meant to assess the influence of social groupings on socio-sexual behavior. When OLI and GRA were housed separately during years seven and eight of life, both subjects were housed with at least one adult male, adult female, and juvenile female; however, only OLI was

housed with other males of a younger age. Given that OLI and GRA did not significantly differ in socio-sexual involvement during year four of life, but OLI spent significantly more time involved in socio-sexual behavior during later years, OLI being housed with younger males could potentially explain his greater involvement in socio-sexual behavior. Though more research beyond the small sample of the present study is needed to provide support for this hypothesis, the present study provides justification that younger, and not necessarily mature males, foster greater opportunities for socio-sexual behavior. This outcome may be due to the potential for male-male bonding stemming from socio-sexual interactions. In bottlenose dolphins, males approaching maturity spend increasing amounts of time with other males of a similar age and eventually form alliances with these males (Connor et al., 2006). Similarly, young male belugas spend more time with other young males than they do with individuals of other age-sex categories (Mazikowski et al., 2018). If these same processes are happening with beluga whales in a captive setting, spending time with males who are closer in age may foster these relationships and be more natural than spending time with and fostering relationships with adult males.

Environmental Factors Influencing Socio-sexual Behavior

Apart from developmental and social influences on socio-sexual behavior, hypotheses of the present study were that month of year and the presence of EEDs would influence the prevalence of socio-sexual behavior, due to the seasonality of mating behavior in belugas and the possible distraction of EEDs, respectively. The results of the present study were not consistent with Glabicky and colleagues' (2010) research. The present study indicated that subjects were more likely to be involved in socio-sexual

behavior during February and May compared to January and more likely to initiate socio-sexual behavior in May compared to January. However, involvement in socio-sexual behavior was relatively consistent across the calendar months, especially from February to June. In contrast, the adult males in Glabicky et al. (2010) thrusted toward adult females mostly during March but thrusted toward other adult males frequently and consistently across the calendar year. The difference in seasonality of behavior may be due to different types of social groupings. The social group studied in Glabicky et al. (2010) consisted of 5 adult males and 7 adult females. This social composition is in direct contrast to the data collected for the present study in which several adult females and only one adult male was present during observation periods.

In regards to the hypothesis that the presence of EEDs would affect socio-sexual behavior, the logistic regression of the present study indicated that the presence/absence of EEDs was not a significant predictor of socio-sexual behavior. Although subjects in the present study could have interacted with EEDs while solo swimming or interacting with another conspecific, the presence of EEDs did not significantly impact the amount of time individuals spent in socio-sexual interactions. This finding supports the use of EEDs in the belugas' enclosure without reservations that EEDs may distract the belugas from engaging in socio-sexual behavior, as typically developing individuals would do naturally.

Implications

The results of this study expand upon the previous description of beluga whale socio-sexual behavior by Hill, Dietrich, and colleagues (2015). Socio-sexual behavior in beluga whales becomes more prevalent over time and the individual behaviors of the

repertoire develop gradually. The finding that the presence of young male conspecifics increases the prevalence of socio-sexual behavior was somewhat unexpected but has important implications. When younger male conspecifics were not present as enclosure mates in the present study, socio-sexual behavior was much less likely to occur. Fewer young males in a population, captive or wild, could mean fewer opportunities to practice socio-sexual behaviors that are crucial to reproduction and survival of that species. Additionally, the consistent and frequent occurrence of male-male interactions into adulthood that have been previously documented (Glabicky et al., 2010), along with knowledge of male-male social bonds in bottlenose dolphins (Connor et al., 2006), suggest that having male conspecifics of a similar age with which to interact is important to the social life of belugas.

As the subjects in the present study have not yet reached adulthood and have yet to potentially reproduce, it remains to be determined if the opportunities to practice socio-sexual behavior increase reproductive success, as has been suggested for socio-sexual behavior in other species (Pruitt et al., 2012). Future research is needed to examine the effects of practice, to determine if belugas form long-term male-male relationships in a similar manner to bottlenose dolphins, and to explore the implications of females participating in socio-sexual behavior during development, but only rarely during adulthood.

Limitations

Several limitations of the present study make it imperative that future data collection is conducted in order to assess further aspects of socio-sexual behavior development in beluga whales. In the present study, the dataset did not contain

observations of some animals during several time frames. While this is unavoidable due to the nature of using archival data and the inherent difficulties surrounding data collection, gaps in the data limit the number of comparisons that can be made. Having continuous data for GRA, like the data that exists for OLI would have allowed for more consistent comparisons between these two individuals. Additionally, the small sample size and lack of data for females overall limits the extent to which conclusions can be drawn regarding sex differences in socio-sexual behavioral development.

Although observational recordings in the present study provided more consistent and clear depictions of socio-sexual behavior than is often possible when collecting data on wild subjects, there were some limitations in the present dataset. Due to the schedules of both the facilities involved and the individuals who collected data, the time of day was not randomly chosen and was most often during earlier morning or later afternoon times. The present study operated on the assumption that the behavior recorded during these times was generally representative of the remainder of the subjects' day. While there are no indications that these recordings are not representative, only 24-hour observations could determine this and such data collection is hindered by logistical and environmental constraints, such as darkness during the night. Finally, even though visibility was generally acceptable during data collection, there are instances where subjects are not visible in video recordings. This constraint was taken into account for data analysis; however, the present study also rests on the assumption that the subjects did not behave in ways that were significantly different while out of sight compared to when they were visible to the camera.

Conclusions

The present study contributes to the literature on socio-sexual behavior in beluga whales by presenting a description of its development and factors that influence its frequency beginning in the fourth year of life. Data from five belugas housed in North American zoological facilities suggest that the frequency of socio-sexual behavior increases throughout development for males and that females are less likely to be involved in socio-sexual behavior compared to males. Additionally, the behaviors of the socio-sexual repertoire change in the frequency of their use over the course of development, with behaviors more critical to sexual reproduction appearing later in development. Across development, the presence of young male conspecifics greatly increased the odds of the subjects in the present study engaging in socio-sexual behavior. This information highlights the potential importance of both wild and captive populations having male offspring, especially if future research finds that the amount of socio-sexual experience prior to maturity affects reproductive success.

APPENDIX A - Operational Definitions of Behaviors

Table A1. *Operational Definitions of Behaviors*

Type of Social Interaction	
Socio-sexual	Interaction in which actor displays any one of the behaviors described by Hill, Dietrich, et al. (2015) to be central to the socio-sexual repertoire. Open mouth behaviors alone were not coded as socio-sexual unless directed at the genital region of the recipient
Agonistic	Interaction in which the actor chases, bites, head jerks, or open mouths at recipient and no other socio-sexual behaviors are displayed
Affiliative	Interactions that are not socio-sexual or agonistic in nature. Includes pair swims and cooperative play with EEDs.
Behaviors	
Open mouth	The actor, while facing another animal, rapidly opens its mouth fully and holds it open for at least 1 second. Mutual open mouth threats do occur.
Bite	The actor visibly places mouth on receiving animal
Head Jerk	The actor makes quick head movement toward recipient
Chase	Actor swims rapidly toward recipient, while recipient swims away from actor
Bubbles	Large exhalation or series of small bubbles released from blow hole
Mirrored Pair swim	Swim in which two animals are faced ventral to ventral with actions that are synchronized and mirrored
Lateral Swim	The actor rotates body so that the pectoral fins are pointed toward the surface
Side Present	The actor positions body parallel with receiver's body and has ventral toward receiver
Pectoral Fin Up	The actor extends pectoral fin away from body so that the fin is perpendicular to the body
Genital Rub	The actor moves its genital region along the receiver's body or object

Erection	Penis is extended externally from the genital slit
Horizontal S-posture	The actor's body is in a lateral swim position with the genitalia thrust forward and the rest of the body following in a curved position with flukes back, static hold for 2-3s
Vertical S-Posture	The actor's body is vertically positioned in the water column in the shape of an S, static hold for 2-3s
Pelvic thrust	The actor pushes genital region toward a recipient
Intromission	The act of the penis inserted into the genital slit

Note: Adapted from Hill, Dietrich, et al. (2015).

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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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 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 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: **17110902**
PROJECT TITLE: **The Development of Sociosexual Behavior in Beluga Whales (Delphinapterus leucas)**
PROPOSED PROJECT DATES: **11/2017 – 09/2020**
PROJECT TYPE: **New**
PRINCIPAL INVESTIGATOR(S): **David Echevarria**
DEPARTMENT: **Psychology**
FUNDING AGENCY/SPONSOR:
IACUC COMMITTEE ACTION: **Full Committee Review Approval**
PROTOCOL EXPIRATION DATE: **September 30, 2020**

Jake Schaeffer, PhD
IACUC Chair

November 9, 2017

Date

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