

**SOCIAL AND NON-SOCIAL PLAY IN BELUGA WHALES (*DELPHINAPTERUS  
LEUCAS*)**

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## **DEDICATION**

To Emma, for all her support and love throughout my education and making sure we always have a *whale* of a time.

## ABSTRACT

Although many species of Cetacea play, few detailed studies of their play exist. The present thesis provides detailed descriptions of two types of social play (sexual play and mouth-to-mouth interaction play) and one type of non-social play (object play) in belugas (*Delphinapterus leucas*), an Arctic dwelling species of toothed whale. The group studied contained animals of many ages of both sexes and was maintained under human care. Given the unique features of different types of play, a major conclusion of this thesis is that play is multi-functional. Indeed, even a single form of play (e.g., mouth-to-mouth interactions) may have more than one function. For example, while mouth-to-mouth interactions may help train motor coordination skills in immature animals, such play may be used to form and maintain social relationships in adults. For belugas, play is serving many functions, all depending on the type of play and the age of the animals.

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## **LIST OF ABBREVIATIONS**

EEDs	Environmental enrichment devices
GA	Georgia Aquarium
MtMI	Mouth-to-mouth interaction
SWoT	SeaWorld of Texas

## CHAPTER 1: GENERAL INTRODUCTION

### 1.1 Why study play?

Play is a behavior that is easily recognized, but rarely described in detail. Although seemingly ubiquitous to human life or even in our domestic pets' lives, play is restricted to only three of the 35 animal phyla (Burghardt, 2005). For two of the phyla (Arthropoda and Mollusca), only a few species have been reported to play (e.g., paper wasps, *Polistes dominulus*; Dapporto et al., 2006; common octopuses, *Octopus vulgaris*; Kuba et al., 2006). Most play behavior occurs in Chordata, or animals with a notochord, and more specifically in the subphylum Vertebrata, with the most play reported in mammal and bird species (Burghardt, 2005). Indeed, even within Vertebrata, the most playful subphylum, not all species engage in play behavior, not even in the most playful class Mammalia (Burghardt, 2005). This raises an unresolved question: why do some animals play and not others?

For animals that do play, they do not all play in the same way (see Burghardt, 2005; Fagen, 1981). Some animals only engage in social play, often characterized as play fighting, or play that involves two or more individuals engaging in play with one another (e.g., kittens, *Felis catus*, wrestling with one another). Some only engage in locomotor play characterized by solo running, jumping, or leaping (e.g., kittens quickly scaling a tree or jumping around), and finally, some only engage in object play where they manipulate objects (e.g., a kitten pouncing on a stuffed toy). Some species engage in all three forms of play, like belugas or white whales (*Delphinapterus leucas*), the subject of this thesis.

Many functions have been proposed for play (Fagen, 1981; Smith, 1978), with some positing immediate benefits and others positing delayed benefits. A proposed delayed benefit of play is that it allows animals to practice behaviors they will use in adulthood (Groos, 1898). Despite this possibly being the case for some species (e.g., Blumstein et al.,

2013), it does not seem to hold true for all species (e.g., Sharpe, 2005). Another delayed benefit is that play provides training for the unexpected, making them more resilient adults, as play exposes animals to unpredictable events (Špinka et al., 2001). For example, Barrett et al. (2021) found that young Javan slow lorises (*Nycticebus javanicus*) engaging in social play fighting often do so with older, skilled males and play while it is raining. By playing with older males, they are engaging in riskier play than if they had played with an unskilled juvenile, and so, are effectively self-handicapping themselves. By playing in the rain, the tree branches they are playing on become slippery, increasing the chances of falling off and getting injured, making the play more challenging.

Rats (*Rattus norvegicus domestica*), which engage in social play frequently as juveniles, seem to be playing when they are young to cope better as adults. Rats that have the opportunity to engage in social play as juveniles have refined executive functions and socio-cognitive skills, both essential for planning and executing complex behavioral sequences (Pellis et al., 2014, 2017; Vanderschuren and Trezza, 2014). In contrast, juvenile rats with limited juvenile play opportunities have altered brain development, specifically in the pre-frontal cortex (Bell et al., 2010; Himmler et al., 2013)—the part of the brain thought to be responsible for executive functions—which seems to lead to reduced executive function and poor adult social skills (Schneider et al., 2016; Stark and Pellis, 2020). Even though the mechanism by which play improves later function has not been proposed, the finding that in several species social play in the juvenile period increases adult reproductive success (Ahloy Dallaire & Mason, 2017; Nunes, 2014; Nunes et al., 2004; Perret, 2021), reinforces the view that play can have delayed benefits.

Several studies have also demonstrated the presence of immediate benefits. Some animals, such as chimpanzees (*Pan troglodytes*), seem to use play to manage their social

bonds. In stressful situations, such as before feeding, chimpanzees engage in play to reduce social tension and reduce aggression (Palagi et al., 2004; Yamanashi et al., 2018). Similarly, bonobos (*P. paniscus*) also engage in more play before feeding (Palagi et al., 2006). For some animals, like bottlenose dolphins (*Tursiops truncatus*), it has been suggested that play aids bond formation (Kuczaj et al., 2006; Mackey et al., 2014). So, at least for social play, there are both delayed and immediate benefits to playing (Palagi, 2011; Pellis and Pellis, 2011).

Because of the potential benefits play affords, cases of play need to be more critically identified. To do so, Burghardt (2005) proposed that for a behavior to be classified as play, it needs to meet five criteria: that (1) it is not completely functional in form or context; (2) it is voluntary and pleasurable; (3) it is structurally or temporally different from the ‘serious’ behavior it resembles; (4) it is performed repeatedly; and (5) it is initiated by healthy, unstressed animals. Applying this 5-criteria definition, researchers have identified play in a variety of species (e.g., cichlids, *Tropheus duboisi*; Burghardt et al., 2015; emydid turtles, *Pseudemys* spp.; Kramer and Burghardt, 2010). By identifying and characterizing play in a wide range of species, we may gain a better understanding of *how* and *why* animals play.

Many mammals play and Cetacea (i.e., whales, dolphins, and porpoises) are no different. From bowhead whales (*Balaena mysticetus*) playing with logs (Würsig et al., 1989) to killer whales (*Orcinus orca*) engaging in self-beaching play (Guinet, 1991), cetaceans engage in many forms of play (see Paulos et al., 2010). Despite reports of species of both Mysticeti (i.e., baleen whales) and Odontoceti (i.e., toothed whales) engaging in social, object, and locomotor play (Paulos et al., 2010), apart from bottlenose dolphins, the play behavior of few species has been described in detail. This is likely due to the

challenges that come with studying aquatic mammals (e.g., low visibility, animals are remote, it is expensive); however, some smaller odontocetes can be reliably housed in managed care and have been for decades. These few species (e.g., *Delphinapterus leucas*, *Lagenorhynchus obscurus*, *Orcinus orca*, *Tursiops* spp.) provide unique opportunities to study play in detail, over long periods of time. One species that has been housed in managed care for decades is the beluga.

## 1.2 Why study belugas?

The beluga is an Arctic-dwelling toothed whale. In wild settings, belugas live in groups of around 5-10 individuals (Hobbs et al., 2000; O’Corry-Crowe et al., 2020), but congregate in the thousands in the summer months (Frost and Lowry, 1990; Lydersen et al., 2001; O’Corry-Crowe et al., 2018). Possessing a relatively large brain (Hof et al., 2005), belugas have complex social lives and live in fission-fusion societies (O’Corry-Crowe et al., 2020). Belugas develop slowly, relying on the support of their mother for the first two to three years of life (Heide-Jørgensen and Teilmann, 1994; O’Corry-Crowe, 2009). Once beluga calves no longer rely on their mothers’ milk, belugas feed on fish, squid, and shrimp as well as other crustaceans found on the seafloor (Doan and Douglas, 1953; Heide-Jørgensen and Teilmann, 1994). Shortly after starting to eat solid food, males and females reach sexual maturity at around 6- to 8-years-old and 4- to 8-years-old, respectively (Heide-Jørgensen and Teilmann, 1994; Robeck et al., 2005). Belugas are slow-moving, swimming at around 2.5 to 6 kilometers per hour in open water and in ice-covered water (Lydersen et al., 2001; Suydam et al., 2001). This makes them suitable prey for polar bears (*Ursus maritimus*) (Freeman, 1973; Lowry et al., 1987; Smith and Sjare, 1990), killer whales (Ferguson et al., 2012; Shelden et al., 2003), and humans (O’Corry-Crowe, 2009). Despite

all of this information, beluga ethology, sociology, and biology, is poorly understood. Indeed, what we do know about wild belugas is restricted to observations made in the summer months as observations are nearly impossible during the ice-covered winter months.

Although some of the basic ethology of belugas is understood, little has been reported on in terms of behavior, especially play behavior. However, the few studies available have reported that belugas engage in social play (e.g., Hill and Ramirez, 2014; Hill et al., 2015a, 2019; Hill and Campbell, 2014; O’Corry-Crowe et al., 2020), object play (e.g., Hill and Ramirez, 2014; Hill, 2009; Hill et al., 2017; Krasnova et al., 2014), and locomotor play (e.g., Hill and Ramirez, 2014). The goal of this thesis is to provide detailed descriptions of both social and non-social play in a group of belugas living in managed care.

### **1.3 Beluga social play**

In the wild, it seems that belugas engage in play with their mother (Karenina et al., 2013; O’Corry-Crowe et al., 2020) and with other juveniles (O’Corry-Crowe et al., 2020). In managed care, belugas play frequently with each other, engaging in sexual play (Hill et al., 2015b; Lilley et al., 2020), chasing (Hill and Ramirez, 2014), mouth-to-mouth interactions (Hill et al., 2019), and rough and tumble play (Hill and Ramirez, 2014). Play, although primarily initiated by juveniles (four times more than adults), is also observed in adults (Hill and Ramirez, 2014).

To gain a better understanding of beluga social play, in this thesis, two types are described and analyzed. The first is socio-sexual play, a type of social play that involves behavior patterns from the affiliative and sexual repertoire (Hill et al., 2015b). A previous

study provided a detailed description of its development from four years of age to adulthood, around 11 years of age (Lilley et al., 2020). At these ages, socio-sexual play makes up a large portion of juvenile and sub-adult belugas' activity budget and is a primary form of socializing. Chapter 2 provides a detailed analysis of the emergence of sexual play behaviors in early development, from birth to three years of age, providing a deeper understanding of the ontogeny of this form of play.

The second is a form of mouth-to-mouth interaction that has been aptly called the “mouth game” (Hill et al., 2019). The mouth game, (Hill et al., 2019) which has been documented/photographed in a variety of beluga populations (e.g., Connor and Peterson, 1994; Krasnova et al., 2014) involves two belugas interlocking their jaws. The preliminary report provided by Hill et al. (2019) detailed the topography of this unusual behavior and characterized the mouth game over the first year of life in four animals. Chapter 3 provides a detailed developmental analysis of this behavior across all ages.

#### **1.4 Beluga non-social play**

Unlike social play, non-social play is performed alone and this type of play seems to occur frequently (Hill and Ramirez, 2014). Non-social play is often directed at or employs objects and/or the environment, and also includes locomotor play. For belugas, locomotor play may consist of rolling around in the water column, jumping out of the water, also known as aerial displays, or surfing on the water, to name a few (Hill and Ramirez, 2014). In object play, they use various parts of their body to manipulate objects found in their environment, which in human care can include environmental enrichment devices, such as balls and towels. Objects of organic origin, like feathers (Hill and Ramirez, 2014a), algae, and logs (Krasnova et al., 2014) are also used when available. Belugas also play with

water—which is described as an object in this thesis—as water is used to create bubble rings (Delfour and Aulagnier, 1997; Hill and Ramirez, 2014; Hill et al., 2011), bubble helices (Jones and Kuczaj II, 2014), small-to-medium singular bubbles (Hill et al., 2011), bubble streams (Delfour and Aulagnier, 1997; Hill et al., 2011), bubble bursts (Hill et al., 2011), and for spitting (Hill and Ramirez, 2014).

Chapter 4 provides a detailed description and analysis of object play, as currently most of the information that is available are anecdotal reports of object play (e.g., Delfour and Aulagnier, 1997; Jones and Kuczaj II, 2014). Given the diversity of actions and objects used, a first step was to develop an ethogram. This ethogram then provides a basis for detailed analysis of sequences of play with objects.

As outlined above, a problem with understanding the functions of play is that there are often contradictory findings—a particular type of play is shown to provide a benefit in one species, but not another (e.g., Blumstein et al., 2013; Sharpe, 2005). Why some species, but not others, gain particular benefits is a major unresolved problem in the comparative study of play. Detailed data on the play of a species from an infraorder that has not been studied extensively (i.e., belugas; Cetacea) provides a broader perspective on the problem, potentially offering clues as to why animals play. Further, belugas make a curious animal to study as they have relatively large brains (Hof et al., 2005; Ridgway et al., 2017) and live in complex social groups (O’Corry-Crowe et al., 2020) similar to primates, such as chimpanzees (e.g., Symington, 1990), making them a useful species to add to comparative analyses. By studying belugas, we gain behavioral information on a rarely studied family, Monodontidae, and seldom studied infraorder of Mammalia, Cetacea, while also learning about aquatic play.

## **CHAPTER 2: THE EMERGENCE OF SEXUAL PLAY IN BELUGAS: FACTORS INFLUENCING ITS DEVELOPMENT**

### **2.1 Introduction**

Social play is a common form of play reported in many species of mammals, birds, reptiles and some arthropods (Burghardt, 2005; Fagen, 1981). Sexual behavior, including aspects of courtship and mating, is incorporated in to the social play of many species (e.g., Berry and Signoret, 1984; Kramer and Burghardt, 2010; Nunes et al., 1999, 2004; Orgeur and Signoret, 1984; Pellis, 1993; Pellis and Pellis, 2018). During the juvenile period in rats, and some other rodents, engagement in such play, especially when it involves competition, can affect the development of the prefrontal cortex and improve socio-cognitive skills (e.g., Baarendse et al., 2013; Bell et al., 2010; Burleson et al., 2016; Marks et al., 2017; Schneider et al., 2016; Stark and Pellis, 2020).

Many cetacean species engage in social play, and it often incorporates sexual behavior (i.e., socio-sexual play) (e.g., Baird, 2000; Brown and Norris, 1956; Connor et al., 1992, 2001, 2006b; D'Agostino et al., 2017; Hill et al., 2015b; Lilley et al., 2020; Mann, 2006; McBride and Hebb, 1948; McBride and Kritzler, 1951; Parks et al., 2007; Sauer, 1963; Serres and Delfour, 2017; Soriano Jimenez et al., 2021; Thomas and Taber, 1984; Würsig, 2009; Xian et al., 2010). For many cetaceans, socio-sexual play is most frequent in the juvenile period and potentially provides several functional benefits, such as forming social bonds (Connor et al., 1992, 2001, 2006a; Lilley et al., 2020; Mann, 2006; Mazikowski et al., 2018; Xian et al., 2010), increasing reproductive fitness (Lilley et al., 2020; Mann, 2006; Parks et al., 2007), and strengthening muscles and increasing coordination (Thomas and Taber, 1984). Given that developmental studies that chart the age of onset, frequency of use of different sexual behavior patterns, and changing patterns

of partner preference can provide clues as to the potential functions of play (e.g., Carter et al., 2019; Himmler et al., 2016; Théoret-Gosselin et al., 2015; Turner et al., 2020), this is the approach adopted in the present paper on the early development of social play in belugas.

Recent studies in captive belugas show that they often engage in socio-sexual behavior (Glabicky et al., 2010; Hill et al., 2015b; Lilley et al., 2020), an activity also reported in wild populations (Lomac-MacNair et al., 2016; O’Corry-Crowe et al., 2009, 2020). This sexualizing of social behaviors, although likely not always play, occurs within playful contexts and in combination with other types of play (Hill and Ramirez, 2014). Adult belugas in managed care engage in socio-sexual behavior throughout the year, but this behavior fluctuates seasonally and mostly occurs between males (Glabicky et al., 2010; Ham et al., 2021b; Hill et al., 2015b; Lilley et al., 2020). Socio-sexual behavior in adult belugas is characterized by four main behaviors: ventral presentation, horizontal/lateral s-posture presentation, genital rub, and pelvic thrust, all of which can occur with penile erection (described by Hill et al., 2015b). These four behaviors can occur independently of each other or in sequence and are often reciprocated (Glabicky et al., 2010; Hill et al., 2015b; Lilley et al., 2020). Hill et al. (2015b) reported that the majority (45%) of all socio-sexual interactions occurred between adult males and juvenile males with both initiating the behavior (41% and 52%, respectively); however, juvenile males initiate 86% of the bouts when interacting with juvenile females (which make up 29% of all socio-sexual behaviors). Beluga socio-sexual behavior observed in managed care animals takes up around 3-10% of their time and occurs in both adults and juveniles and in both sexes. Socio-sexual behavior in belugas may manage social bonds (Glabicky et al., 2010; Hill et al., 2015b; Lilley et al., 2020) similar to bottlenose dolphins (*T. aduncus*) (Mann, 2006).

Further, socio-sexual behavior might play a role in mating, courtship, and reproductive success—both by facilitating the development of mating behavior (Lilley et al., 2020) and as practice to ensure successful intromission (Glabicky et al., 2010); however, all of these suggestions require further investigation. Given the frequency of socio-sexual behavior, its role in socializing, and its potential consequences on mating, it is important to understand its development, as this can provide clues as to whether the emergence and maturation of specific behavior patterns is optimal for the presumed functions (Carter et al., 2019; Fagen, 1977).

The first study to characterize the development of beluga sexual behavior examined the development from age four to adulthood in a managed care population (Lilley et al., 2020). This study found that, as belugas age, they engage in more socio-sexual behavior, it becomes more complex (e.g., pelvic thrusts significantly increase with age), and that juveniles were more likely both to initiate sexual play and be involved in sexual play when other male belugas were present. Males engage in more socio-sexual behavior than their female juvenile counterparts. One juvenile male tracked from age 4 to age 10 increased its sexual play with every year of life (with a slight decrease in year 7), with it peaking at 8 years of age and then slowly decreasing. Juveniles younger than 4 years old also engaged in sexual play, although it did not appear to be as stereotypical as juvenile or adult sexual behavior. For example, in younger animals, genital rubbing is often incorporated into an energetic social play called ‘riding’ or ‘mounting’, in which young belugas try to ride the back of their conspecifics. Also, during locomotor play, calves may raise their pectoral fin much like the adult s-posture sexual presentation, but without the associated posturing (Hill et al., 2015b).

Although Lilley et al. (2020) described the development of sexual play in juveniles, the early onset and ontogeny of these play behaviors remains unknown. Understanding how behaviors emerge can help explain, at least in part, the potential functions of the behaviors, as the age at which the play achieves its mature form may indicate when it is most likely to serve its adaptive functions (Pellis et al., 2010). For example, while the frequency of social play in juvenile rats can be influenced by maternal interactions at earlier ages (primary literature reviewed in Himmler et al., 2016), pre-juvenile playful experiences with either the mother or siblings have minimal influence on the development of juvenile-typical play (Himmler et al., 2015; Siviý et al., 2017). It is only when social play achieves the fully juvenile-typical form, that such play has the most influence on the development of socio-cognitive skills (Pellis et al., 2014; Vanderschuren and Trezza, 2014). The early development of many types of behavior is often piecemeal.

An example of such piecemeal development is dust bathing in chickens (*Gallus gallus*). This involves a series of behavior patterns in which chickens move dust through their feathers in order to clean them (Hogan, 2001). The components of this dust bathing sequence continue to develop in a piecemeal fashion until the chick is able to execute the full adult sequence (i.e., behavior A in the sequence emerges before behavior B). In addition, this pattern of maturation proceeds in the same manner whether the chicks experience dust particles or not - that is, the chicks do not need to rehearse the components for the sequence to be completed (Vestergaard et al., 1990). This piecemeal pattern of development has been documented in several behaviors in other species (e.g., exploration: Eilam and Golani, 1988; grooming: Golani and Fentress, 1985; displays: Groothuis, 1989; bird song: Marler, 1987, 1991; righting: Pellis et al., 1992; Pellis et al., 1991). Piecemeal development may be widespread because it is less costly to develop a behavior system over

time rather than immediately at the age the system is needed (Pellis and Pellis, 2009; Williams, 1992).

Whether the socio-sexual play of belugas and other cetaceans develops in a piecemeal manner is unknown. In part, this is likely due to the difficulty of observing animals consistently, especially in the wild. In managed care, belugas provide an opportunity to explore this issue. If, like social play in rats or dust bathing in chickens, the piecemeal development of socio-sexual play emerges in a rigid or orderly manner in belugas, it would imply that the adaptive value of the behavior is limited to an older age, when the play reaches its full repertoire (Lilley et al., 2020). However, if the appearance is less rigid, with marked variation across individuals, it would imply that the calves may gain valuable experiences from engaging in this behavior at an earlier age. As well as the pattern of onset of play, developmental changes in the partners selected for play may also provide differential opportunities for gaining beneficial experiences (Turner et al., 2020). Such partner preferences are present in juvenile belugas (Lilley et al., 2020), but it is unknown whether they exist earlier in infancy.

For many species of primates, when infants first begin to engage in social play, they do so with their mothers, then gradually switch to playing with similar aged peers (e.g., Fröhlich et al., 2020; Hanby, 1976; van Lawick-Goodall, 1968). In contrast, in many other animals, such as rodents (Burlison et al., 2016; Cramer et al., 1990; Pellis and Pellis, 1997; Thiels et al., 1990) and cats (e.g., Barrett and Bateson, 1978; West, 1974), from the outset, play is primarily directed to peers rather than the mother. In bottlenose dolphins, it seems that, when they are first starting to engage in sexual play (as early as a few days old), young calves do so with both their mothers and peers (Mann, 2006; Mann and Smuts, 1999). Play partner preferences, excluding the mother, can be influenced by the dominance status (e.g.,

Cheney, 1978; Lutz et al., 2019; Pellis and McKenna, 1992) and sex (e.g., Brown and Dixson, 2000; Eaton et al., 1985; Krzyszczyk et al., 2017; Maestripieri and Ross, 2004; Mann, 2006; Most and Strum, 2020) of the potential partner.

The present study examined the pattern of emergence of sexual play behaviors in belugas over the first three years of life. While partner availability can influence the amount of sexual play (Lilley et al., 2020), it remains unknown as to whether the onset of specific behaviors depends on the availability of suitable play partners. Similar to Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) (Xian et al., 2010), we predicted that calves would prefer to play with their mothers in the first year of life, and then begin to diversify their play partners to include their peers. This expansion of play partnerships was expected to first be extended to age-matched peers and then, with age, include older males (Lilley et al., 2020). We predicted that sexual play would increase with age and that there would be a sex difference, with males initiating more sexual play than females, like the juvenile animals described by Lilley et al. (2020). However, this sex difference could arise in two distinct ways: (1) the sex difference in initiation of sexual play would be evident from the earliest onset of play, or (2) the sex difference begins to emerge as the calves shift their attention from engaging in play with their mother to engaging with their peers.

## **2.2 Methods**

### *2.2.1 Subjects*

Nine beluga calves, born and housed at SeaWorld of Texas (SWoT), were observed between 2007-2019. The calves were born between 2007 and 2017 and were housed within a relatively stable population that included at least one immature beluga within a few years of the same age and several other adult (both male and female) and sub-adult belugas, depending on the year (for descriptive information, see Table 2.1). The beluga pod

inhabited seven interconnected pools holding approximately 2 million gallons of water. Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) were also housed within this facility and usually occupied the pools adjacent to the belugas at any given time. Pacific white-sided dolphins were occasionally housed in the same pool as the belugas. Social compositions changed daily. Belugas were also provided with environmental enrichment devices (EEDs) at varying times of the day and for varying lengths throughout the study period. EEDs consisted of buoys, balls, ropes and a combination of similar objects.

### *2.2.2 Data collection*

Data were collected via video recordings from 2007 to 2019 at SWoT, when the calves were between 0-3 years of age (for behavior after this age, see Lilley et al., 2020). 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 (Altmann, 1974). The data collection method was approved by the Institutional Animal Care and Use Committee at St. Mary's University.

**Table 2.1***Relevant demographics and available data.*

Subject	Birthdate	Data Start Date	Data End Date	Age (months) Start	Age (months) End	Sex
OLI	6/23/2007	6/24/07	6/17/10	1	36	M
GRA	6/26/2007	6/26/07	6/24/10	1	36	M
QIN	7/31/2008	8/07/08	10/31/10	1	28	F
BEL	6/12/2009	6/13/09	5/29/12	1	36	F
ATL	6/23/2010	6/26/10	6/3/13	1	36	F
SAM	7/9/2013	7/22/13	6/24/16	1	36	M
STE	7/26/2013	7/27/13	11/12/15	1	28	F
KEN	8/11/2016	8/18/16	7/29/19	1	36	M
INN	9/17/2017	9/18/19	9/8/19	1	24	M

For the present study, two videos per month for each individual subject were selected from a video archive. 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 571 videos, which represented 135 h.

### 2.2.3 Video analysis

Videos were scored for the measures and behaviors listed in Appendix A. Of particular note, genital rubbing, riding, pelvic thrusting, ventral presenting (both s-posture and vertical and horizontal), and erections, as identified by Hill et al. (2015b), were classified as sexual play. If scan samples were used because focal follows were unavailable, only the first 15 min was scored. The initiator and recipient of each sexual play interaction were noted. Additionally, all non-sexual social playful interactions, affiliative and agonistic

interactions were scored. The presence or absence of environmental enrichment devices (EEDs), the age of subjects, and the identity of all other subjects present in the same enclosure was recorded for each video. Sex and age class of other individuals were scored as: calf (birth to 3 years-old), juvenile (4- to 6-years-old), sub-adult (7- to 10-years old), and adult (over 11-years-old).

#### *2.2.4 Statistical analysis*

Because video length and the number of video recordings available for each calf varied, for comparisons across animals, the rate of sexual play was calculated. This was achieved by dividing the frequency with which calves engaged in specific behaviors by the total observation time. Rates were calculated with different total observations times depending on the question being asked. For example, total observation time for seasonality was calculated by using the total observation time per month, whereas total observation time for behavioral development would be the total time observed in each six-month block.

To test if other factors influenced the calf's involvement and initiation of sexual play a logistic regression was performed including multiple variables: the sex of subject, the sex and age of the animals housed with the calf, and if EEDs were present. To determine if there were differences between the sexes, a Student's t-test was used. To determine if there were differences between subjects in the initiation of sexual play, an ANOVA was employed.

In order to determine if there was a seasonal effect on sexual play, rates were generated based on the calendar month and plotted. To compare males and females, these rates were standardized by dividing the monthly rate by the total rate throughout the year to generate a percentage or proportion of sexual play for each month. To test if the rate at which beluga calves engage in sexual play changes with development, an ANOVA was

used to compare the rate of sexual play in which beluga calves engaged in six-month developmental blocks. This was done for both males and females.

To test if the behaviors used in sexual play changed with age, behaviors used in play bouts for both males and females were calculated as a percentage. This demonstrated how their behavioral repertoire changed through development. Finally, to examine how partnership changed through development, egocentric, unidirectional social networks were created for both males and females. Because these networks are unidirectional and egocentric, they only demonstrate the partners with whom the calves chose to initiate sexual play and not play that was directed to the calves by others. Dyads were categorized by sex and age categories: calf, juvenile, sub-adult, and adult. We plotted both the ‘actual’ frequency with which beluga calves engaged with their conspecifics for each year of life as well as a ‘when available’ social network. Because the animals with whom the calves were housed varied from day-to-day there was not an equal representation of each age/sex category and so the ‘when available’ networks show if there was a preference for an age/sex category when they had access to those individuals. The ‘when available’ metric used in the social networks was calculated by dividing the frequency of interactions with the age/sex category by the total observations where that age/sex category was present. This provides both an accurate depiction of which animals they interacted with, as well as described if they had a preference for an age category and/or sex when they were housed with that age/sex group. Social networks were created in R (R Core Team, 2020) using the package *igraph* (Csardi and Nepusz, 2006). All of the statistical analyses were performed using R and all graphs were plotted with R employing the package *ggplot2* (Wickham, 2016).

## 2.3 Results

### 2.3.1 Presence and order of emergence of sexual play behaviors

By 36 months of age, not all calves were observed performing all elements of their sex-typical sexual repertoire (Table 2.2). All males engaged in sexual play that incorporated genital rubs, ventral presenting, riding, and horizontal s-posturing, but only SAM and INK engaged in all of the behaviors, which also included thrusting, vertical s-posturing, and erections (Table 2.2). All female calves engaged in sexual play that incorporated genital rubs, ventral presenting, and riding, with STL adding horizontal s-postures. Only BEL engaged in all of the sexual behaviors, which also included horizontal s-posturing, thrusting, and vertical s-posturing (Table 2.2).

The sequence in which sexual behaviors emerged was fairly consistent, with genital rubs emerging first for 7 of the 9 calves, with thrusts, s-posturing, and penile erections being the last to emerge (Table 2.3). For OLI and GRA, vertical s-postures and penile erections did not emerge until after the calves were 36 months old, however, it is possible that these behaviors were not captured on camera. While the age of onset of specific behaviors consistently differed—for example, genital rubs ( $M \pm SD = 2.1 \pm 1.3$  months) emerged much earlier than erections ( $36.3 \pm 17.7$  months)—there was considerable individual variation in the specific age of onset (as indicated by the large SDs versus means).

**Table 2.2***Presence or absence of sexual play behaviors in calves across the first three years of life.*

Animal	Sex	Behavior						
		Genital Rubs	Ventral Present	Riding	Horizontal S-Posture	Thrust	Vertical S-Posture	Erection
OLI	M	+	+	+	+	-	-	-
GRA	M	+	+	+	+	+	-	-
SAM	M	+	+	+	+	+	+	+
KEN	M	+	+	+	+	+	+	-
INK	M	+	+	+	+	+	+	+
QIN	F	+	+	+	-	-	-	N/A
ATL	F	+	+	+	-	-	-	N/A
BEL	F	+	+	+	+	+	+	N/A
STL	F	+	+	+	+	-	-	N/A

**Table 2.3**

*The sequence of emergence of sexual play behaviors in calves across the first three years of life.*

Animal	Sex	Behavior						
		Genital Rubs	Ventral Present	Riding	Horizontal S-Posture	Thrust	Vertical S-Posture	Erection
OLI	M	1*	1*	2	3	4 <sup>†</sup>	5 <sup>†</sup>	4 <sup>†</sup>
GRA	M	2	1	3	5	4	-	6 <sup>†</sup>
SAM	M	1	4	2*	5	3	2*	6
KEN	M	1	3	2	4	5*	5*	-
INK	M	1	2	3	4*	5	4*	6
QIN	F	1*	2	1*	-	-	-	N/A
ATL	F	1*	1*	2	-	-	-	N/A
BEL	F	1*	1*	1*	4	2	3	N/A
STL	F	2	1	3	4	-	-	N/A

*Note.* \*Indicates behavior emerged in the same month of life. <sup>†</sup>Emerged after 36 months of age.

### 2.3.2 *Factors influencing the occurrence of sexual play*

A binary logistic regression model, using data from all subjects, was tested to determine the relationship of several factors that could influence the involvement of calves in sexual play. The model predicted the subject's involvement in sexual play using the predictor variables of sex of subject, presence of EEDs, and age and sex of conspecifics housed with the focal animal (Table 2.4). The model found that being male significantly predicted involvement in sexual play as did being housed in the same enclosure with adult and sub-adult males.

A second binary logistic regression model was tested to determine the relationship of several factors that could influence the initiation of sexual play in calves. The model predicted the subject's initiation in sexual play using the predictor variables of sex of subject, the presence of EEDs, and the age and sex of conspecifics housed with the focal animal (Table 2.5). The model found that calves were significantly more likely to initiate sexual play if they had either an adult male or a male calf housed in the same enclosure.

Throughout the first three years of life (Figure 2.2), males initiated more sexual play than females,  $t(27) = 2.0$ ,  $p = 0.025$ . When comparing the males with one another using an ANOVA, all of the males engaged in sexual play at a similar rate except for INK, who engaged in significantly more than all of the other male calves,  $F(4, 23) = 3.95$ ,  $p = 0.01$ . An ANOVA for the females calves showed no significant difference,  $F(3, 18) = 1.07$ ,  $p = 0.387$ .

**Table 2.4***Factors of the model predicting the involvement of the subject in sexual play.*

Factors	Exp (B)	95 % CI for Exp (B)		p-value
		Lower	Upper	
Male Subject	1.04	1.01	1.06	0.002*
EED Present	0.98	0.95	1.01	0.283
Adult Male Present	1.07	1.04	1.09	< 0.001*
Adult Female Present	1.23	0.84	1.82	0.290
Sub-adult Male Present	1.07	1.05	1.09	< 0.001*
Sub-adult Female Present	0.96	0.90	1.01	0.111
Juvenile Male Present	1.00	0.98	1.02	0.846
Juvenile Female Present	0.96	0.88	1.04	0.278
Calf Male Present	1.00	0.98	1.02	0.873
Calf Female Present	1.00	0.99	1.02	0.625

*Note.* \* $p < 0.05$

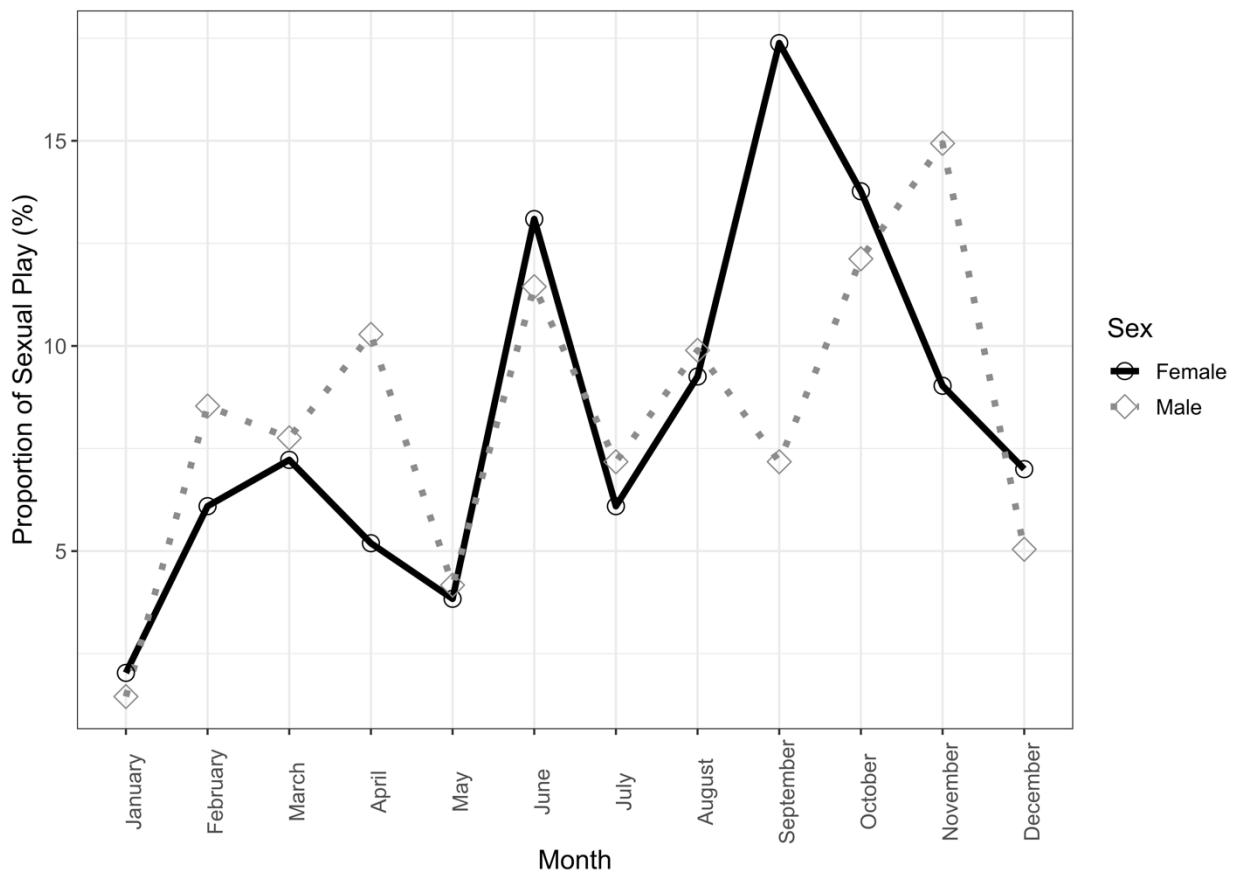
**Table 2.5***Factors of the model predicting the subject initiating sexual play.*

Factors	Exp (B)	95 % CI for Exp (B)		<i>p</i> -value
		Lower	Upper	
Male Subject	1.02	0.999	1.03	0.061
EED Present	0.99	0.959	1.03	0.665
Adult Male Present	1.03	1.01	1.05	0.015*
Adult Female Present	1.23	0.92	1.65	0.152
Sub-adult Male Present	1.02	0.99	1.05	0.119
Sub-adult Female Present	0.96	0.91	1.01	0.129
Juvenile Male Present	0.99	0.96	1.02	0.429
Juvenile Female Present	1.00	0.96	1.05	0.834
Calf Male Present	1.02	1.00	1.05	0.034*
Calf Female Present	0.99	0.97	1.02	0.708

*Note.* \*  $p < 0.05$

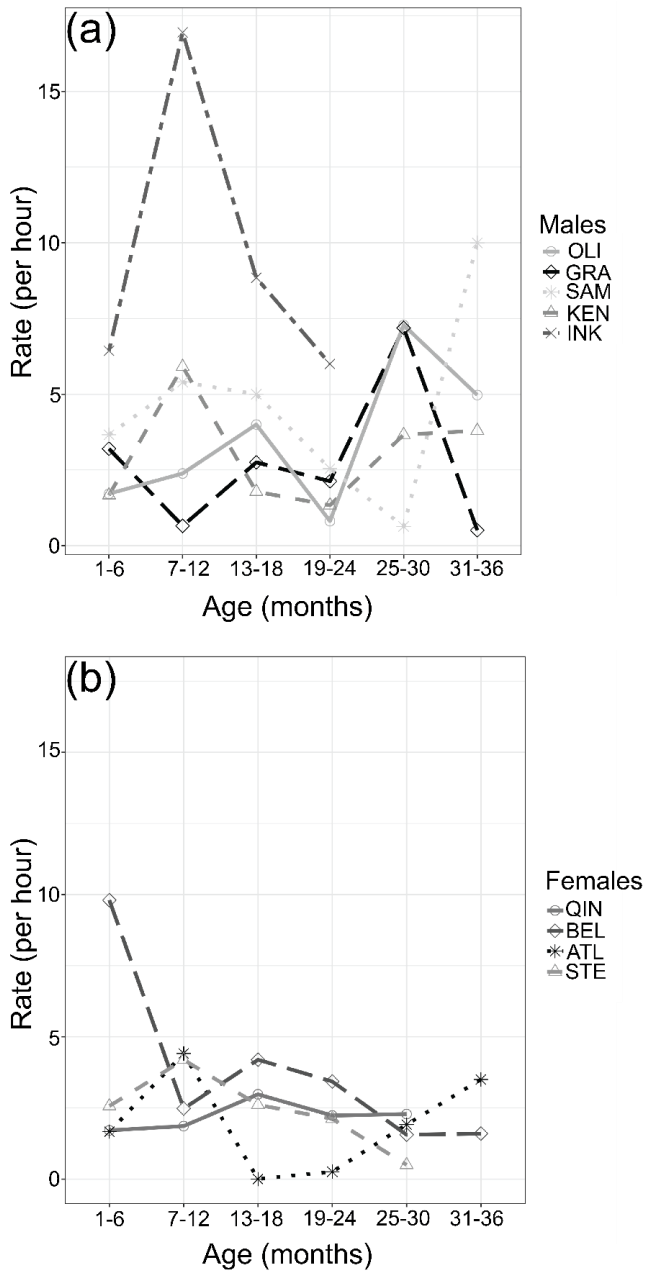
### 2.3.3 Seasonality and time spent engaging in sexual play

To determine if there was a seasonal effect on the initiation of sexual play in beluga calves, the proportion of the time sampled that calves engaged in sexual play was calculated for each month (Figure 2.1). Male calves engaged in the most sexual play in November (15% of all sexual play) and the least in January (1%). Female calves engaged in the most sexual play in September (17%) and the least in January (2%).



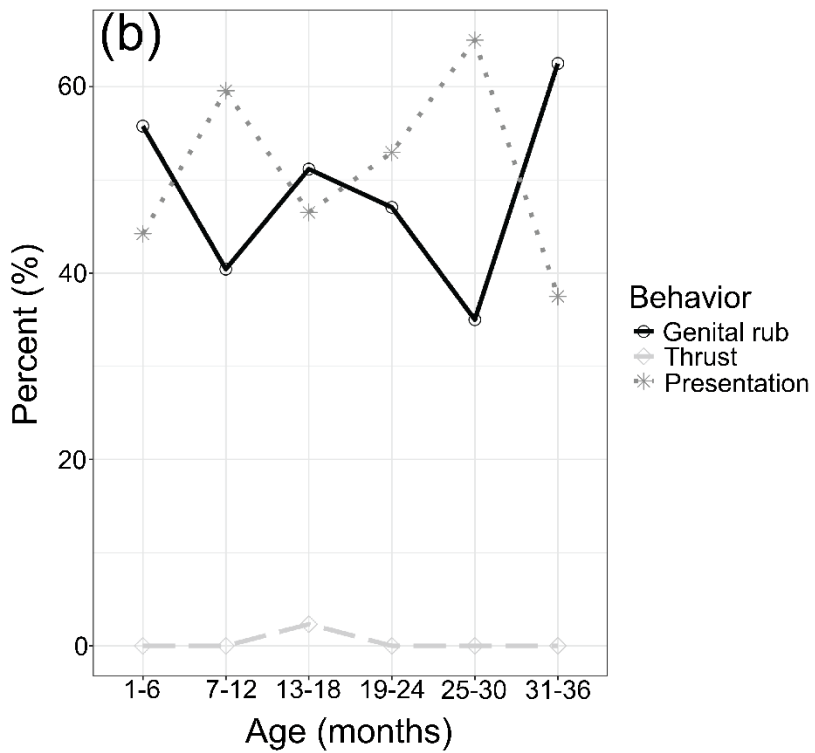
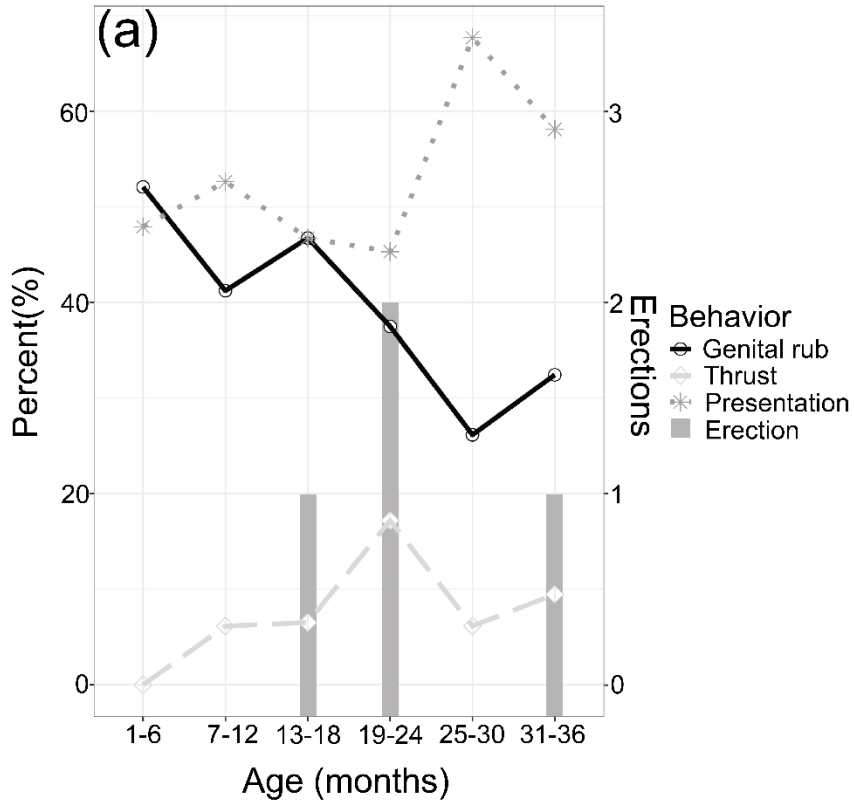
**Figure 2.1** Seasonal changes in sexual play behavior.

Comparing the rate of engaging in sexual play across the six month blocks (Figure 2.2), showed no age-related change in either males  $F(5, 22) = 0.60, p = 0.70$  or females  $F(5, 16) = 0.67, p = 0.65$ .



**Figure 2.2** Rate at which male (a) and female (b) calves initiate sexual play in six-month blocks.

For male calves, the type of sexual play behaviors in which they engaged changed as they aged, whereas that of females stayed relatively the same (Figure 2.3). To compare between the sexes, the percentage of sexual play behaviors (genital rub, pelvic thrust, presentation, and erections as identified by Hill et al., 2015b) was calculated to determine what behaviors they were using when engaging in sexual play across the first 3 years of life. As males aged, thrusting increased along with presenting, while genital rubbing decreased. Erections did not occur frequently, and only SAM and INK were observed with erections. For females, genital rubbing and presenting remained fairly consistent across ages, with each behavior making up around 50% of their sexual play.



**Figure 2.3** Percentage of behaviors that comprise sexual play for both male (a) and female (b).

### 2.3.4 Play partners

To determine if there was a correlation between the age of the initiator and the age of the receiver in sexual play, we used Kendall's Tau, as the data were not normally distributed (Shapiro Wilks  $p < 0.05$ ). The age of the receiving animal was significantly and negatively correlated with the age of the calf initiating sexual play, suggesting that the calves engaged in socio-sexual play with older individuals ( $r_{\tau} = -0.08$ ,  $p = 0.004$ ).

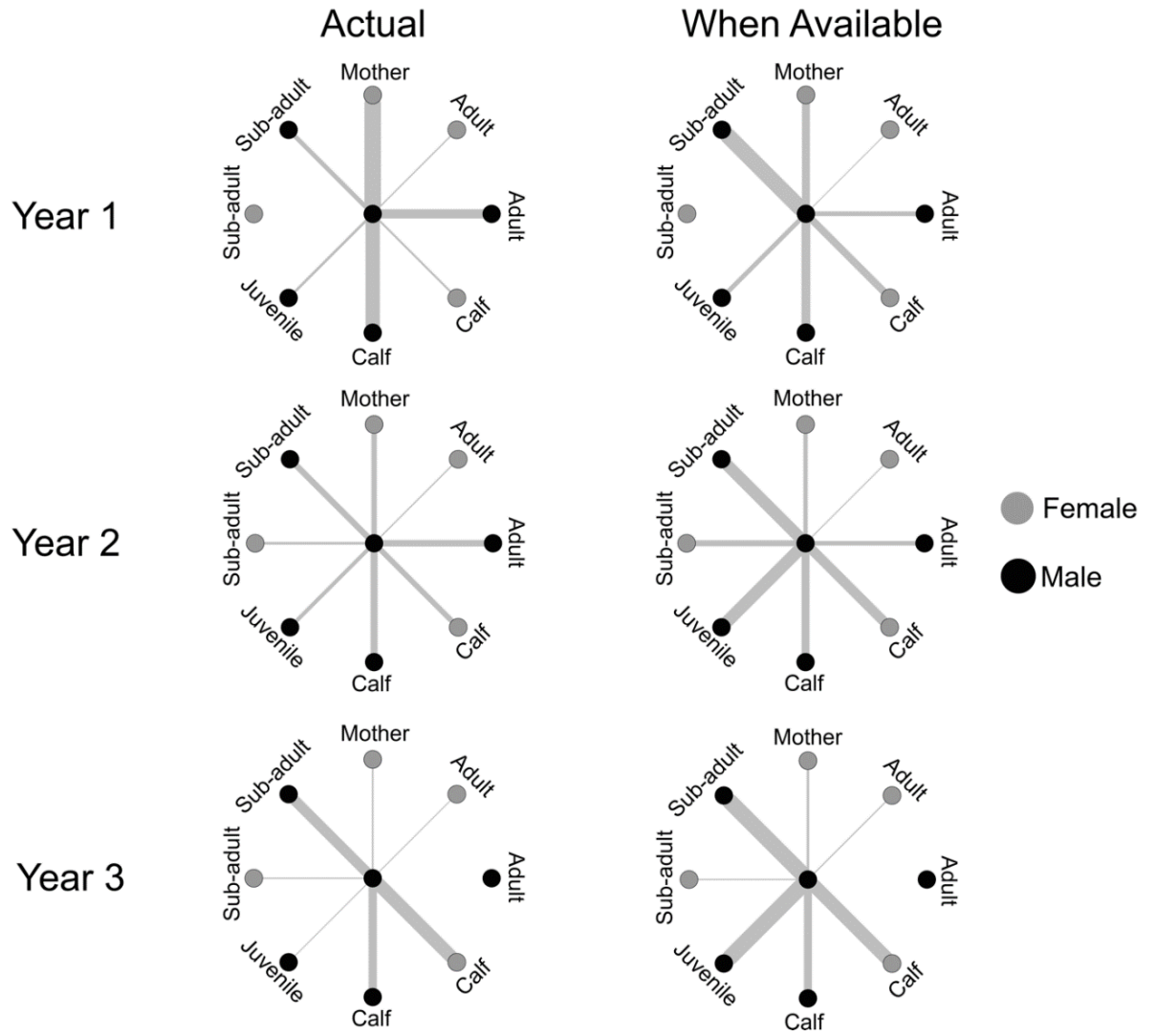
Social networks were created to see if there was a partner preference and if it changed with development. Individual partner preferences were combined for both male and females to generate the social networks (Figures 2.4 and 2.5). To determine if there was a change in partner preference with age, we looked at the first, second, and third years of life.

#### 2.3.4.1 Males

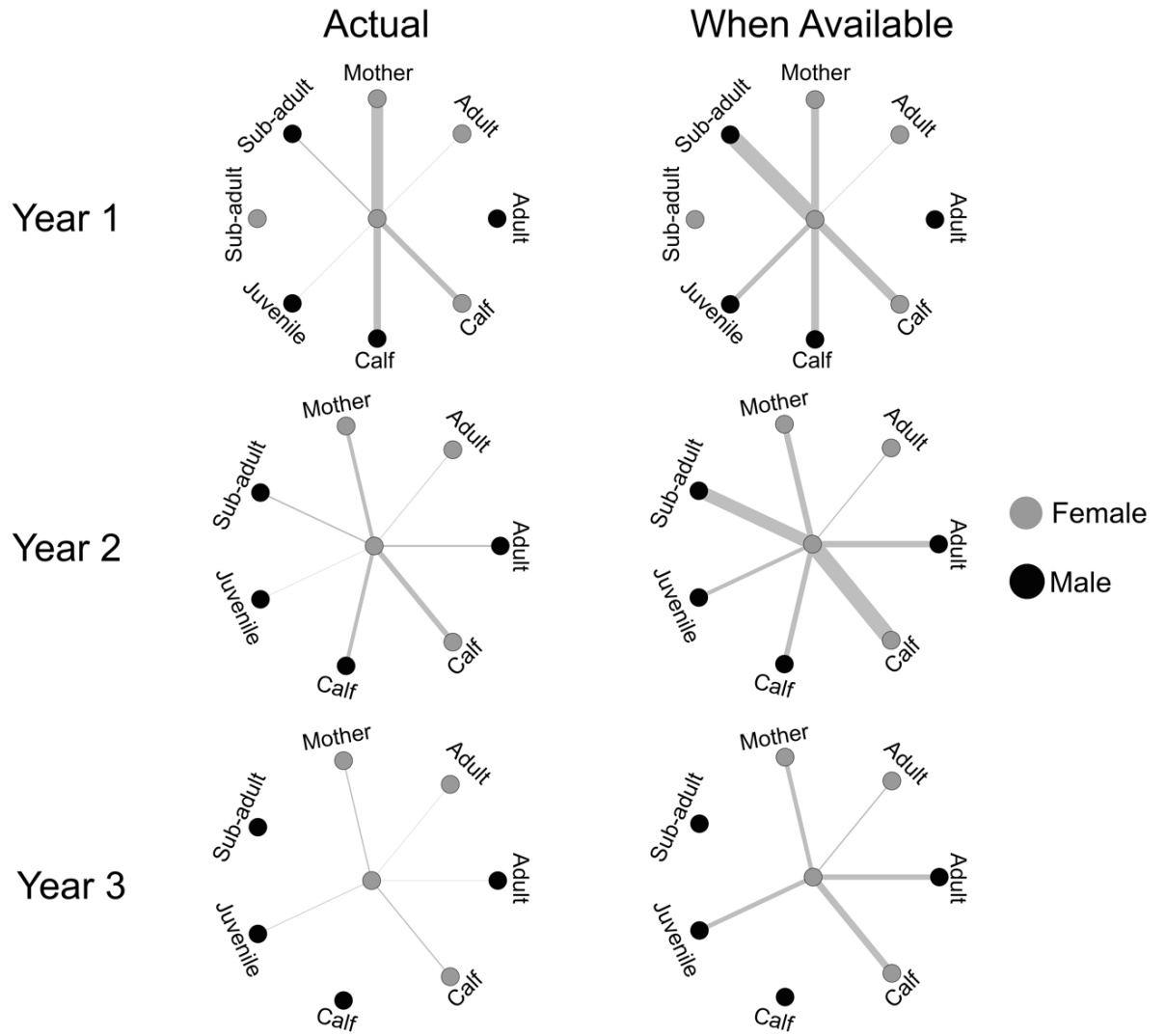
Social networks revealed that males in their first year of life mostly interacted with calves of the same age and sex and with their mother, but when available, calves had a preference for sub-adult males (Figure 2.4, top panels). Sexual play directed towards their mother occurred far less often in the second year of life with sexual play being directed at all age and sex categories relatively equally, but, again, when given the option, male calves preferred to interact with both older juvenile and sub-adult males (Figure 2.4, middle panels). Finally, in their third year of life, sexual play with their mother was even less frequent, with most directed towards other calves and to sub-adult males, but, consistent with the first two years, when available, male calves preferred to initiate sexual play with older males (Figure 2.4, lower panels). Although not their preferred partners, with increasing age, male calves increasingly played with female calves (Figure 2.4).

#### 2.3.4.2 *Females*

Using social networks for female calves, it was found that females in the first year of life direct the majority of sexual play towards their mother, and, to a lesser degree, to other calves of both sexes. However, when available, female calves preferred sub-adult males (Figure 2.5, top panels). In their second year, sexual play was distributed fairly equally across age/sex categories with a slight bias for other calves and their mother, but when available, female calves preferred to play with other female calves and with sub-adult males (Figure 2.5, middle panels). In their third year, female calves initiated play fairly equally between their mother, female calves, and juvenile males, but when available, play was preferentially directed towards adult males; however, the strong preferences observed in the first two years of life were greatly reduced.



**Figure 2.4** *Unidirectional egocentric social networks of male calf sexual play.*



**Figure 2.5** *Unidirectional egocentric social networks of female calf sexual play.*

## 2.4 Discussion

Belugas frequently engage in socio-sexual play, both in captivity (Glabicky et al., 2010; Hill et al., 2015b; Lilley et al., 2020) and in the wild (Lomac-MacNair et al., 2016; O’Corry-Crowe et al., 2009, 2020), but detailed studies are few, with only one paper to date characterizing the development of socio-sexual behavior from 4 years of age to adulthood (Lilley et al., 2020). The present study aimed to add to this literature by describing the emergence of socio-sexual play as well as the developmental and social factors that influence these behaviors from birth to 3 years of age.

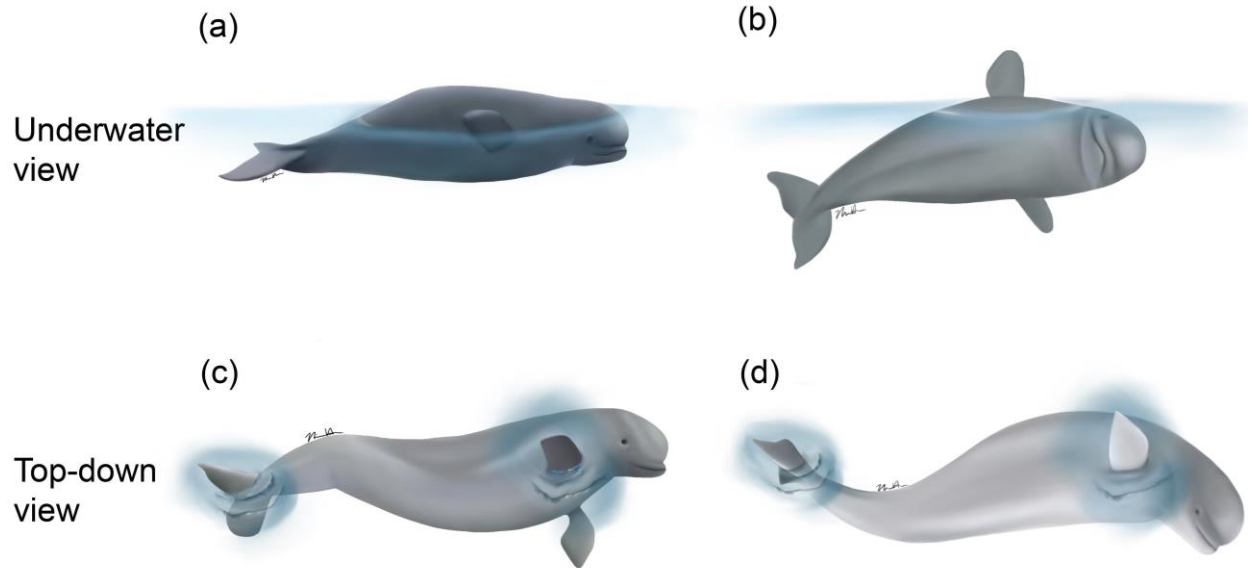
As in the case of dust bathing in chickens (Hogan, 2001), the order of emergence of sexual behavior patterns in belugas was the same for all the calves observed, suggesting that the behavioral components in the sexual sequence likely develop regardless of experience. However, whereas the order of emergence of socio-sexual behaviors was rigid, the variation in the age of onset across individuals points to the possibility that particular social experiences are involved in facilitating their emergence (Tables 2.2 and 2.3). Such variation suggests possible environmental stimuli being important for causally facilitating when a component emerges, even if it does not emerge unless the previous component in the sequence has. For example, despite OLI and GRA following the same pattern of emergence in their socio-sexual behavior patterns, OLI was not observed engaging in thrusts, vertical s-postures, or penile erections until after 36 months of age, and GRA did not develop vertical s-postures and erections until after 36 months of age and was never observed to engage in vertical s-postures (however, he was moved to a different facility at 43 months and so was not observed past that age). Both OLI and GRA did not have access to older juvenile, sub-adult or adult males until they were 24 months old, indicating that the presence of older males may be an important factor in facilitating the emergence of

these behaviors. This possibility is supported by INK, who was housed with the 4 other males (1 male calf, 1 male juvenile, 2 male adults), and developed all the behaviors before he was 24 months old. This suggests that, although sexual behaviors emerge regardless of experience (i.e., they are not learned), increased social arousal caused by the presence of older males, may influence the speed at which behaviors emerge. Indeed, when available, older males were preferred play partners (Figures 2.4 and 2.5).

The presence of older males may increase social arousal and the amount of socio-sexual behavior performed (Horback et al., 2010; Lilley et al., 2020), and perhaps facilitate the speed of maturation of sexual behavior patterns (present study). This would not be unlike the development of displays in black-headed gulls (*Larus ridibundus*), which like the socio-sexual behavior of belugas, develop in a piecemeal fashion (Groothuis, 1989). To develop these displays fully, the chicks need to engage in aggressive interactions with conspecifics (Groothuis, 1992), but it is not that they learn how to shape effective displays during these interactions, but rather, it is that the encounters stimulate the release of testosterone, and it is the testosterone that facilitates the maturation of the displays (Groothuis and Meeuwissen, 1992). That is, the social interactions indirectly influence the rate development by altering hormone levels (see also Wommack and Delville, 2007). Further, social behavior in immature belugas fluctuates seasonally, and seems to do so in concert with the fluctuation of hormones (Ham et al., 2021b). An alternative mechanism could be that, as belugas are able to mimic motor actions of conspecifics (Abramson et al., 2017), calves may learn motor behaviors by imitating adult behavior (Krasnova et al., 2009), with a greater number and range of older males being present increasing the opportunity to observe behavior patterns most salient to them at different ages. However, the rigid order of emergence of sexual play behaviors makes this possibility less likely.

There is a third mechanism that could account for the order of appearance of these behavior patterns.

The piecemeal, but orderly, emergence of socio-sexual behavior may arise the way it does because simpler components need to develop earlier, before these can be combined into more complex actions. For example, thrusting behavior incorporates lateral presenting, s-posturing, and genital rubbing, all of which emerge before thrusting does. How they present to partners provides a framework for how such complex behavior emerges. Based on observations made during the detailed analyses of video recorded sequences for the present study, ventral presentations occur in the first couple of months after birth, while vertical and horizontal s-postures emerge in the third and fourth months, respectively. The development of the horizontal s-posture has several distinct phases (Figure 2.6). Initially, the young beluga raises its pectoral fins above the water while it is parallel to the water surface with its ventrum facing downward (a), later, the beluga rotates 90° around its longitudinal axis, holding its pectoral fin closest to the surface out of the water (b), later still, while maintaining a horizontal position relative to the surface, not only does the young beluga raise its fins, but it also begins to contort its body in ways resembling the s-posture (c), finally, while maintaining the horizontal orientation with its pectoral fin out of the water, it can create the 's' shape with its body (d). Detailed kinematic analyses are needed to document the age-related changes in each of the socio-sexual behaviors fully and how they are combined, but as the example described above illustrates, the order of emergence could be a function of how the behavior patterns are assembled and combined. Both social facilitation through arousal and social imitation could contribute to the process.



**Figure 2.6** *The development of s-postures as demonstrated by INK. In the first stage, INK raises his pectoral fin while remaining horizontal with his ventrum facing the bottom (a), later, in the second stage, this is transformed into a lateral present in which he holds his pectoral fin completely out of the water while turning his whole body 90° (b). In the third phase, INK begins to contort his body into crude versions of the s-posture (c). Finally, in the fourth stage (d), INK is able to form the 's' shape with his body, completing the adult typical horizontal s-posture presentation. Illustrations by Nichole Ham.*

Irrespective of which of these mechanisms, or combination of mechanisms, best accounts for the orderly, but variable emergence of the socio-sexual repertoire, from a life history perspective (Fagen, 1974), the main developmental finding in the present chapter is that it is not until the animals are 3-4 years of age that the full repertoire of behaviors is present. Not only is this developmental milestone reached before sexual maturity (Robeck et al., 2005), but this timing also has implications for the possible functions of socio-sexual play in belugas.

#### *2.4.1 The functions of socio-sexual play*

For many species, the functional benefits of social play on adult sexual competency (e.g., Ahloy Dallaire and Mason, 2017; Goy and Wallen, 1979; Nunes, 2014; Perret, 2021) and socio-cognitive skills in general (e.g., Baarendse et al., 2013; Burlison et al., 2016; Schneider et al., 2016; Stark and Pellis, 2020) arises from the play performed in the juvenile period when all the behavioral components are present (Himmler et al., 2016). If belugas follow this pattern, it would seem likely that it is after the full socio-sexual repertoire is in place (3-4 years of age) that performing socio-sexual play would be beneficial in training sexual and social skills. Observations of one Yangtze finless porpoise calf, led the authors to suggest that developing in the presence of other individuals has a beneficial effect on future reproduction (Xian et al., 2010), but without controlled experiments, such suggestions are speculative and inconsistent with studies from non-cetacean mammal species. Based on the evidence available, it would seem likely that socio-sexual play would have its main adaptive benefits in the juvenile period when the repertoire is complete and this form of play is most frequent (Lilley et al., 2020).

Studies in either the wild or in captivity are needed to track whether belugas that gain their socio-sexual repertoire earlier and/or engage in this behavior more frequently are

more sexually and socially skilled as adults, as has been found in gray mouse lemurs (*Microcebus murinus*) (Perret, 2021) and Belding's ground squirrels (*Urocitellus beldingi*) (Marks et al., 2017; Nunes, 2014). Another possible function may be that socio-sexual interactions with group members could be important for forming early bonds with conspecifics, as is the case with bottlenose dolphins (Connor et al., 2006b; Harvey et al., 2017). A recent study has suggested that male-male bonding can occur through socio-sexual behavior in young belugas with patterns of affiliation emerging within the first five years of life (Mazikowski et al., 2018). Not only would such a function not be limited to the age when the socio-sexual repertoire is fully mature, but it could also explain why development is faster in groups with more variation in individuals. The attraction of older males as socio-sexual play partners at all ages (Lilley et al., 2020; present study) may reflect the importance of establishing relationships with more dominant members of the group, relationships that could be useful for later alliances. From a husbandry perspective, these findings highlight the importance for having diverse social groups of belugas (Halteman and Ryan, 2019; Hill and Nollens, 2019), especially for the young.

Evidence from the wild suggests that beluga social groupings vary seasonally, both in the number of animals and in demographics (O'Corry-Crowe et al., 2018, 2020). Interestingly, there is evidence that some beluga populations form juvenile subgroups (Krasnova et al., 2009, 2014) composed of calves of multiple ages and from different maternal lineages, allowing the opportunity to play with many different partners (O'Corry-Crowe et al., 2020). If, as seems likely, having diverse social experiences is important to facilitate development, a potential function of pods congregating into larger groups may be to allow immature belugas greater opportunity to play. If so, this is not unlike the case of

normally solitary orangutans (*Pongo* spp.), in which mothers congregate, allowing their offspring to play (Fröhlich et al., 2020; Noordwijk and Arora, 2012).

One prediction we made was that beluga calves would mostly play with their mothers in the first year of life, and then slowly diversify to age matched partners and then to older play partners over the subsequent two years. This is what was found for both male and female calves (Figures 2.4 and 2.5). This mother-calf play preference in the first year of life has also been reported in Yangtze finless porpoises (Xian et al., 2010), killer whales (Guarino et al., 2017), and bottlenose dolphins (Mackey et al., 2014; Mann & Smuts, 1999). However, when the opportunity arose, both male and female calves preferred to engage with sub-adult males, even in the first year. As in most cases, dyadic play in mammalian species mostly occurs between partners of similar age and/or size (e.g., Byers, 1980; Gomendio, 1988; Mackey et al., 2014; Maestripieri and Ross, 2004; Palagi, 2006), the finding of a preference for playing with older males from as early as the first year was unexpected. Animals playing with older or larger animals put themselves at a disadvantage as older or larger animals may be more skilled, stronger, and/or dangerous (Barrett et al., 2021; Carter et al., 2019; Petru et al., 2009). In some cases, however, there may be an advantage to such a mismatch. Interacting socio-sexually with older partners may facilitate sexual development (Brown & Dixson, 2000; Hanby, 1976), and more vigorous playful competition may provide the opportunity to gain skills from more experienced partners and better learn to cope with unpredictable events (Barrett et al., 2021; Špinka et al., 2001).

#### 2.4.2 *Unexplained partner preferences*

Descriptively, the rate at which male and female calves engage in sexual play with their mother decreases dramatically after the first year of life as calves start to initiate play with partners of different ages and sex categories. Similarly, bottlenose dolphins change

their partner preference in social play with age (which includes sexual play) from their mother, to age matched peers, to older conspecifics (Mackey et al., 2014). When beluga calves are initiating sexual play, both male and female calves seem to prefer female partners when playing with age matched calves. This preference for female calf partners was unexpected as most beluga juvenile play is between age matched males (Lilley et al., 2020). Bottlenose dolphins calves of both sexes also have a significant preference for interacting with male calves over female calves in sexual play (Mann, 2006). The deviation from the trend reported here might be accounted for by the small sample size and limited partner choice. Despite play occurring between age matched partners, when available, male beluga calves initiated most of their play with older animals (i.e., juveniles and sub-adults). In contrast, female calves engaged in most of their behavior with age matched animals until their third year of life when much of their partner preference is lost. A similar sex difference in social dynamics has been described between male and female juvenile bottlenose dolphins, where males interact with more varied social partners than females (Galezo et al., 2020).

For male calves, a logistic regression found that they were significantly involved in more sexual play when sub-adult or adult males were present (Table 2.4), suggesting that they are the preferred partners. One explanation for this preference may be that because older animals initiate sexual play more often with male calves, the male calves prefer to play with previous play partners (i.e., older males). Although it only accounts for 6% of the variance, a significant negative correlation was found between the age of the initiating animal and the age of the receiving partner, suggesting that young belugas like to play with older animals and older animals like to play with younger animals.

### 2.4.3 *Sex differences*

Sex differences, which have previously been reported for beluga behavior (e.g., Glabicky et al., 2010; Ham et al., 2021b; Hill and Ramirez, 2014; Hill et al., 2015b, 2018b; Lilley et al., 2020; Mazikowski et al., 2018; Panova et al., 2017), were observed in the present study. As discussed above, there were differences in partner preferences between male and female calves, but there were also other differences in the sexual behaviors of male and female calves. Two hypotheses were posited to account for sex differences in play: that (1) there would be a difference from the onset of such play or (2) sex differences would begin to emerge as calves shifted their attention from playing with their mother to other conspecifics. Although males initiated more sexual behavior than females over the first three years, the behavior in the first year of life was similar between the sexes. Sex differences emerged in the second year of life, when calves shifted from mostly playing with their mother to other members of the pod. This finding is consistent with our second hypothesis.

Although not all males engaged in all six sexual behaviors (Table 2.2), most initiated horizontal s-postures, vertical s-postures, and thrusts. In contrast, only two of the four females initiated horizontal s-postures, while only one female was observed thrusting and initiating vertical s-postures. While females engaged in the same behaviors fairly consistently throughout their first three years of life, in males, some behaviors increased and others decreased (Figure 2.3). For example, in males, thrusting increases while genital rubbing decreases. These sex differences in calf play might reflect differences in adult behavior, as mature male belugas engage in thrusting regularly while females do not (Glabicky et al., 2010; Lilley et al., 2020). Also, as adults, males engage in far more sexual activity than females (Hill et al., 2015b). Similar sex differences, with males initiating more

sexual play than females, have also been documented in other species (e.g., Brown and Dixson, 2000; Eaton et al., 1985; Maestriperi and Ross, 2004; Most and Strum, 2020), including bottlenose dolphins (e.g., Krzyszczyk et al., 2017; Mann, 2006).

While some sex differences may be common across many species, there can also be marked intra-sexual species differences. For example, compared to bottlenose dolphins, belugas seem to develop sexual behaviors at a slower rate. In a population of wild bottlenose dolphins, male calves were observed with erections within the first two weeks of life (Mann and Smuts, 1999). The belugas reported in this study were not observed with erections until they were at least 14 months old. Thrusting was also observed at a much younger age in bottlenose dolphins compared to belugas, with dolphins thrusting at just 2 months old (Mann and Smuts, 1999) and belugas first starting to thrust at 9 months old. Overall, the onset of male sexual behavior is much slower in belugas compared to bottlenose dolphins.

## **2.5 Conclusion**

This study expands upon previous descriptions of the development of socio-sexual behavior in beluga whales in managed care (Hill et al., 2015b; Lilley et al., 2020). Based on this study, we suggest that sexual behaviors develop in a piecemeal fashion, with simple behaviors (e.g., genital rubs and lateral presents) developing before more complex behavior patterns. Like bottlenose dolphins (Mann, 2006), this study found that young males participate in more sexual play than females, and also initiate more adult-typical behavior patterns (e.g., s-posture presents, pelvic thrusts). These sexual play behaviors change in their frequency with age and seem to be influenced by environmental factors such as social partner availability and social arousal. Future research should explore if adult reproductive

success is related to the frequency and emergence of calf sexual play behaviors to determine if early sexual play experiences have a delayed benefit.

## **CHAPTER 3: PLAYFUL MOUTH-TO-MOUTH INTERACTIONS OF BELUGAS (*DELPHINAPTERUS LEUCAS*) UNDER HUMAN CARE**

### **3.1 Introduction**

Physical contact is an important component of social interactions in mammals (Ewer, 1967). Social contact or touch includes affiliative contact, such as mother-infant contact, socio-sexual or copulatory contact and social grooming, and aggressive contact (Hill et al., 2016). The vast majority of affiliative social contact research has investigated mother-offspring contact and its role in the formation of social bonds and infant development (Harlow, 1958; Nakamura and Sakai, 2014). Touch is used to form bonds between mothers and their offspring as well as to facilitate the cognitive, physical, and social development of the young. For many species, social contact continues to be important throughout their lifetime. For example, in primates, social contact often occurs through allogrooming, which strengthens bonds between individuals and is used to mediate post-conflict interactions (Palagi et al., 2006; Romero et al., 2011). Similarly, juvenile Japanese macaques (*Macaca fuscata*) engage in social play that strengthens their social relationships with their conspecifics (Shimada and Sueur, 2018), and male juvenile bottlenose dolphins engage in socio-sexual contact that result in life-long bonds (Connor et al., 1992, 2001, 2006b). Affiliative physical contact between conspecifics is important for many mammals (Dunbar, 2010; Pellis and Pellis, 2010) and this seems especially true for cetaceans.

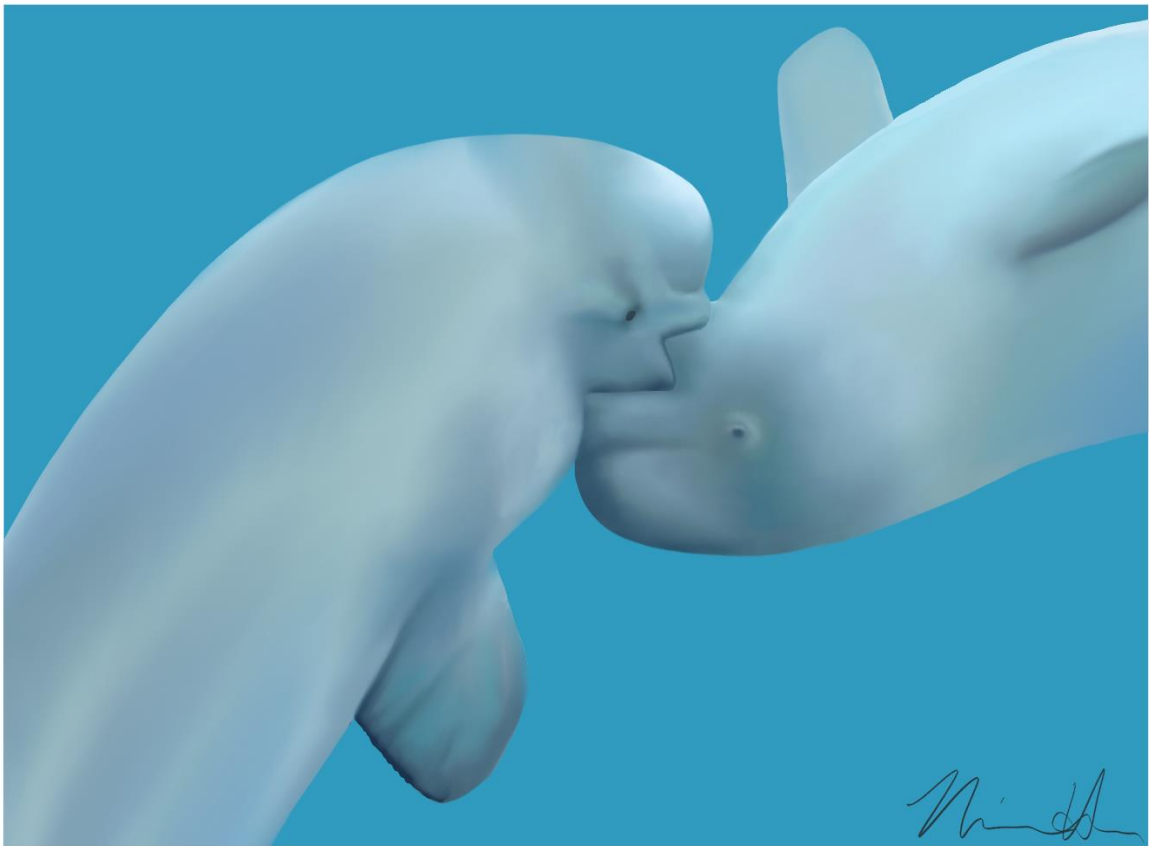
Many species of cetaceans are very tactile (e.g., *Eschrichtius robustus*; Jones and Swartz, 1984; *Eubalaena glacialis*; Kraus and Hatch, 2001; *Orcinus orca*; Guarino et al., 2017; *Phocoena phocoena*; Keener et al., 2018; *Sotalia guianensis*; Izidoro and Le Pendu,

2016; *Stenella frontalis*; Dudzinski et al., 2010; *S. longirostris*; Silva-Jr et al., 2005; *Steno bredanensis*; Yeater et al., 2013; *Tursiops* spp.; Dudzinski et al., 2010, 2012). Observations on cetaceans in both managed care and the wild indicate that contact occurs relatively frequently between conspecifics during affiliative social interactions and often involves various forms of fin and body contact (Connor et al., 2006b; Dudzinski et al., 2009, 2010, 2012; Dudzinski, 1998; Herman and Tavolga, 1980; Mann and Smuts, 1999). One common type of contact, pectoral fin rubbing, may reduce conflict and strengthen bonds similar to that of social grooming in primates (Dudzinski, 1998; Dudzinski et al., 2010; Mann and Smuts, 1998, 1999; Nakamura and Sakai, 2014; Norris, 1991). Further, physical contact with conspecifics is essential for juvenile social development (Dudzinski et al., 2012; Hill et al., 2016; Paulos et al., 2008) as it facilitates bond formation and allows animals to practice social behaviors. Cetaceans also use their mouths in both aggressive and affiliative tactile contexts (Dudzinski, 1998; Frick, 2018; Horback et al., 2010; Kuczaj II and Yeater, 2007; Overstrom, 1983). These interactions include raking with the teeth (aggressive) (Ham et al., 2021a) and gentle mouthing (affiliative) (Hill et al., 2015b). The most unusual, and understudied, use of the mouth is in social interactions involving mouth-to-mouth contact.

Mouth-to-mouth contact has been observed in only a few species of cetaceans. For example, killer whales in human care use mouth-to-mouth tongue touching during affiliative interactions (Bain, 1986; Martinez and Klinghammer, 1978; Nakamura and Sakai, 2014; Sánchez-Hernández et al., 2019). Although rare, mutual mouth contact has also been observed in Atlantic bottlenose dolphins, in human care (Overstrom, 1983) and in the wild (Connor et al., 2000). Young belugas also engage in mouth-to-mouth contact (Hill and Ramirez, 2014; Hill et al., 2019).

Despite the observation of mouth-to-mouth interactions (MtMIs) in a few species, a detailed study of such interactions has yet to be conducted. Beluga MtMIs satisfy Burghardt's (2005) five criteria for play as MtMIs are: (1) not completely functional in either form or context; (2) voluntary and/or pleasurable; (3) structurally or temporally different from the similar 'serious' behavior; (4) performed repeatedly; and (5) MtMIs are initiated by healthy animals. That MtMIs are a form of play fighting is likely in that these interactions fulfill at least some of the criteria proposed by Smith (1997). These are that (1) the play is not over access to resources; (2) the animal invited to engage in play fighting could refuse and not engage; (3) there is often two involved; (4) there is little interest from non-participants; (5) a stronger or older animal will often self-handicap and not use their full strength and restraint is shown by participants; (6) participants may take turns; and (7) participants often stay together in another activity following a play fight. One criterion described by Smith (1997) that could not be verified for belugas was if there are facial and/or vocal expressions made by the animals during the play fighting encounter as the water that belugas inhabit obstructs observations of both. MtMIs have been reported in belugas in several groups in managed care (Harbin Polerland, Qingyun, 2013; MarineLand of Canada, Hill et al., 2019; New York Aquarium, Connor and Peterson, 1994; Vancouver Aquarium; Recchia, 1994) and for one group in the wild (Krasnova et al., 2014). In a preliminary study of the development of calf MtMIs, it was found that this behavior emerges within the first few months of life and occurs sporadically among calves in their first year and is a type of playful social game (Hill et al., 2019). Indeed, This behavior involves two belugas approaching one another in a face-to-face orientation and interlocking their mouths together, as if shaking hands with their mouths (Figure 3.1). Successful mouth-to-mouth contact would seem to require considerable inter-animal coordination, and

for this reason, it was suggested that the experience of MtMIs could be important in the development of physical and social skills (Hill et al., 2019).



**Figure 3.1** *An illustration of a mouth-to-mouth interaction in which one animal interlocks their jaw with another, as if they were shaking hands with their mouths. Illustration by Nichole Ham.*

MtMIs resemble the play fighting reported in many mammals in which partners compete to gain an advantage over one another (Aldis, 1975). But for playful fighting to remain playful, both partners have to have the opportunity to gain that advantage at least sometimes, and this requires that the animals also cooperate (Pellis and Pellis, 2017). Balancing competition and cooperation requires considerable inter-animal coordination of movements, and it is the experiences derived from such coordination that appear to be the ones derived from play, which are critical in training social skills (Pellis et al., 2017, 2019a). Therefore, it is not unreasonable to hypothesize that the cooperation needed to coordinate movements during MtMIs in beluga calves provides comparable opportunities to improve social skills. Given how little is known about MtMIs, an important starting point is to understand their developmental milestones, including partner preferences and how these may change with age.

In the present chapter, we provide a detailed study of mouth-to-mouth play behaviors in a group of belugas observed over a 12-year study period, expanding on the initial report by Hill et al. (2019). We describe the frequency at which these behaviors occur and explore whether there are age or sex biases. As MtMIs are a type of social play, we also explore if there were a preference for partners of a particular age and/or sex. To determine if there were individual differences among belugas, the engagement of MtMIs across multiple years of observation was plotted. By examining the social play of whales across all ages, the developmental time course of MtMIs could be mapped. Finally, because MtMIs are sporadic, the occurrence of the behavior across the calendar year was recorded to determine if this behavior is correlated with seasonal increases in social behavior (Ham et al., 2021b), and thus, whether MtMIs are a by-product of increased sociality. A better understanding of the developmental changes in the frequency of MtMIs and the presence

of partner preferences provide a basis for considering the possible functions of such interactions.

## **3.2 Methods**

### *3.2.1 Subjects*

The animals used in this study were belugas housed at SWoT. The subjects consisted of 9 (4 females, 5 males) juveniles born at SWoT and 10 (7 females, 3 males) adults. Animals were observed from 2007-2019. All the animals were housed with several other individuals with social groupings changing daily based on facility activities and staff decisions. Table 3.1 summarizes the date of birth and dates of data collection, as some animals were not at the facility for the whole 12-year study period. When two calves were transferred to Georgia Aquarium (GA), we continued recording their behavior at the new facility for a limited time (Table 3.1).

The animals at SWoT were housed in a series of seven, connected pools that hold approximately 2 million gallons of water. Pacific white-sided dolphins were also housed within this facility and usually occupied the pools adjacent to the belugas at any given time. At GA, subjects were housed in an approximately 800,000 gallon habitat comprised of three, interconnected pools along with a few other belugas and harbor seals (*Phoca vitulina*).

**Table 3.1***Demographics on juvenile belugas followed in this study.*

Subject	Sex	Location	Birthdate	Data Start Date	Data End Date
OLI	M	SWoT	6/23/2007	6/24/2007	1/8/2019
GRA	M	SWoT	6/26/2007	7/25/2007	11/8/2010
		GA		4/30/2013	2/18/2015
QIN	F	SWoT	7/31/2008	8/26/2008	11/15/2010
		GA		11/12/2013	3/4/2015
BEL	F	SWoT	6/12/2009	6/8/2009	6/14/2013
ATL	F	SWoT	6/23/2010	6/29/2010	2/12/2014
SAM	M	SWoT	7/9/2013	7/19/2013	7/29/2019
STL	F	SWoT	7/26/2013	8/10/2013	11/03/2015
KEN	M	SWoT	8/11/2016	8/15/2016	7/29/2019
INK	M	SWoT	9/17/2017	9/18/2017	7/4/2019

### 3.2.2 Data collection

Data were collected via video recordings from 2007-2019 at SWoT and from 2013 to 2015 at GA. Video recordings included following focal animals and scan samples (Martin and Bateson, 2007), with some recordings taken from above the water and some below the water through a viewing window. Scan samples typically lasted 20 min and aimed to capture the behavior of several individuals at one-minute intervals. Focal follows lasted 15 min and followed the behavior of one individual for the entirety of the video. The same focal follow protocol was implemented at GA. The Institutional Animal Care and Use Committee at St. Mary's University approved the data collection. Observations were conducted primarily at SWoT and several of these subjects were genetically related to some extent.

Videos were sampled for the presence of MtMIs, based upon recorded notes provided in an archived log or notes collected during scoring of archived videos for other

behaviors. Additional videos were randomly selected for social interactions in an attempt to examine at least three videos per month during our 12-year sample period. This additional video selection process enabled the sample to be evaluated for both the occurrence of MtMIs and overall social behavior. Out of the 144 months examined, 77 months had more than 3 videos available, and for 7 months, only 2 videos were available. Videos were recorded between 0600 and 1800, when trainers were absent, and the sample included recordings spread across the day. In total, the present study consisted of 555 videos, which represented 142 h.

### *3.2.3 Video analysis*

Videos were scored for social behaviors (excluding mother-calf social interactions) and for mouth-to-mouth interactions (as described in Appendix B) for belugas of all ages. MtMIs were identified according to the description provided by Hill et al. (2019) and were considered to be a type of play fighting as they followed Burghardt's (2005) five criteria of play and satisfied Smith's (1997) criteria of play fighting. J. Ham scored most of the videos, with additional videos scored by M. Lilley, R. Wincheski, J. Lelekach, J. Miranada, and A. Velarde. Interactions were evaluated for duration, initiator and receiver, and the type of interaction. Belugas were identified via individual physical characteristics by the observer recording the video. Information regarding the ages of the initiator and receiver and the identity of all other subjects present in the same enclosure was also recorded. The ages of the belugas were grouped into three categories: calf (0-36 months-old), juvenile (37-96 months-old), and adult (97+ months-old). Animals were considered to be age-matched if they were born within 24 months of each other.

### 3.2.4 Statistical analysis

To determine if age was correlated with the occurrence of MtMIs (for both animals initiating and receiving the behavior), Kendall rank correlation co-efficient test (tau) was used after finding that the data were non-normally distributed using a Shapiro-Wilk test ( $p < 0.05$ ). The data were then plotted in R (R Core Team, 2020) using the package *igraph* (Csardi and Nepusz, 2006). Kendall's tau was also used to determine if there were correlations between the age of initiator and receiver. To determine if there was a correlation between the age of onset of MtMIs and the age of onset of other social behaviors, the Kendall correlation test was also used given that all of the behaviors were non-normally distributed (Shapiro-Wilk  $p < 0.05$ ). The p-values were corrected using a Bonferroni correction using the *FSA* package (Ogle et al., 2021).

To determine the average frequency of social behavior over the course of the year, we divided the total number of social bouts in a month by the total observation time of the corresponding month, combining the whole 12-year observation period. The frequency of social behavior was calculated for both male and female belugas and was then plotted against the number of MtMIs per month. To determine if there was a correlation between overall female sociality and the occurrence of MtMIs, we used the Kendall correlation test after finding the data to be non-normally distributed (Shapiro-Wilk  $p < 0.05$ ). The same was done with overall male sociality and male MtMIs but using a Pearson's correlation test as the data were normally distributed (Shapiro-Wilk  $p > 0.05$ ). Finally, the number of MtMIs initiated by each calf was plotted against the total number of months observed to compare the rate at which animals initiate MtMIs. This was plotted with R using the package *ggplot2* (Wickham, 2016).

### 3.3 Results

#### 3.3.1 Frequency

A total of 155 MtMIs were observed over the 12 years of observation initiated by 11 different individuals. Due to unclear video footage, 6 MtMIs were observed with an identifiable initiator but an unidentified receiver and so were removed from the partner analyses. MtMIs made up 13.8% of all social play bouts ( $n = 1,120$ ) that were observed in this study.

#### 3.3.2 MtMIs participants

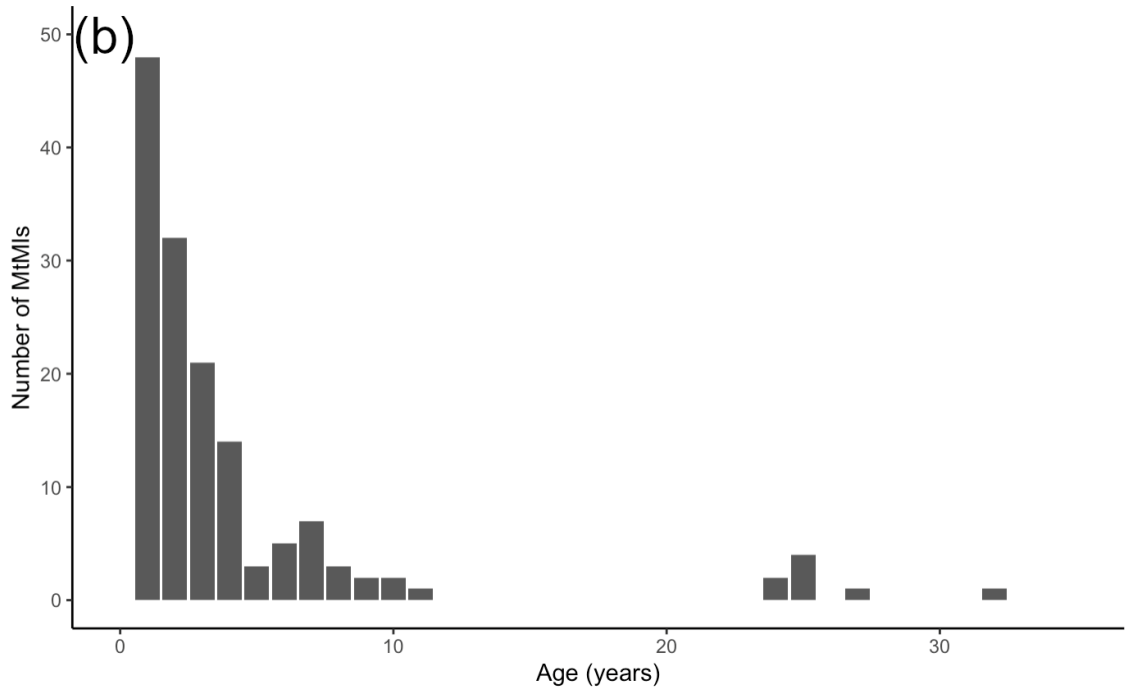
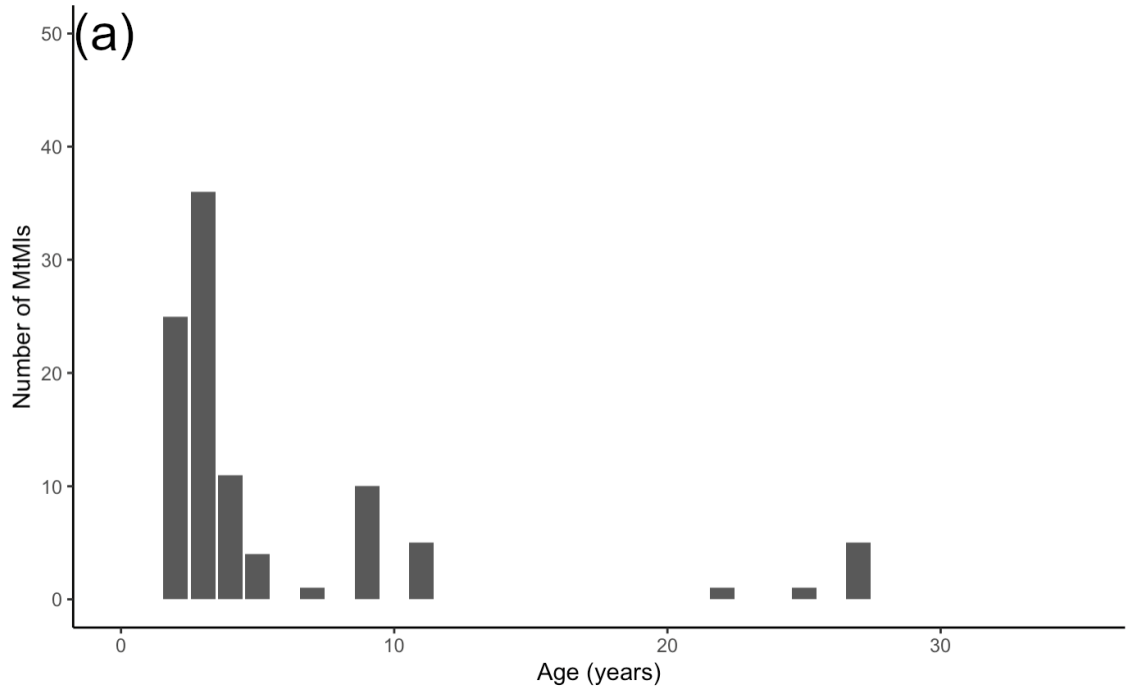
##### 3.3.2.1 Age

The age of the belugas was plotted against the number of mouth games observed by all of the animals (Figure 3.2). Most of the animals initiating MtMIs were calves (75.4%,  $n = 117$ , Table 3.2), with juveniles (10.3%,  $n = 16$ ) and adults (14.3%,  $n = 22$ ) initiating a similar amount. Most of the receivers were also calves (68.5%,  $n = 102$ ), followed by juveniles (22.1%,  $n = 33$ ), then adults (9.4%,  $n = 14$ ). MtMIs significantly declined with age for both initiators ( $r_{\tau} = -0.40$ ,  $p = 0.007$ ) and receivers ( $r_{\tau} = -0.50$ ,  $p = 0.0001$ ).

**Table 3.2**

*Summary of mouth-to-mouth interactions (MtMIs) seen in calves.*

Subject	Sex	MtMI Total	Age of First MtMI (months)
OLI	M	31	3
GRA	M	20	2
QIN	F	9	5
BEL	F	23	2
ATL	F	21	11
SAM	M	22	3
STL	F	9	6
KEN	M	7	19
INK	M	6	6



**Figure 3.2** Age (in years) when mouth-to-mouth interactions were initiated (a) and received (b).

### 3.3.2.2 Sex

When excluding adults from the sex comparisons, as only males initiated MtMIs ( $n = 22$ ), immature females initiated slightly fewer MtMIs than immature males (female  $n = 62$ , male  $n = 71$ ). The mean individual initiation between males ( $M = 14.40$ ,  $SD = 7.44$ ) and females ( $M = 15.50$ ,  $SD = 7.55$ ), however, was not significantly different ( $t(7) = 0.22$ ,  $p = 0.83$ ). With regard to receiving MtMIs, immature females received fewer ( $n = 56$ ) than did immature males ( $n = 79$ ), however, this was not statistically significant ( $t(7) = 0.30$ ,  $p = 0.77$ ) between the mean initiation of males ( $M = 15.80$ ,  $SD = 8.84$ ) and females ( $M = 14.00$ ,  $SD = 8.76$ ). Adult females did not initiate MtMIs but did receive mouth contacts ( $n = 5$ ) similar to adult males ( $n = 9$ ).

### 3.3.3 Partnerships

Because there was day-to-day fluctuation regarding which animals were housed together, partnerships were evaluated by considering the age and sex of other partners housed in the same enclosure with the initiating animal.

#### 3.3.3.1 Age

The majority of MtMIs (71.1%,  $n = 106$ ) occurred between age-matched partners. However, for adults, only 27.3% of the 22 MtMIs initiated were directed to other age-matched adults ( $n = 6$ ). Only 6.5% ( $n = 7$ ) of immature initiated MtMIs were between non-age-matched partners when age-match partners were available. When immature interactions were not between age-matched partners, 23.8% ( $n = 5$ ) were with younger individuals and 76.2% ( $n = 16$ ) were with older partners. Immature animals that were engaging in MtMIs with older animals were doing so mostly with adults ( $n = 14$ ), and most of these were directed to animals other than their mother (78.6%,  $n = 11$ ). A significant Kendall correlation ( $r_{\tau} = 0.45$ ,  $p < 0.0001$ ) was found between the age of the initiator and

the age of the receiver, indicating that belugas prefer to perform MtMIs with age-matched partners.

### 3.3.3.2 *Sex*

Most of the MtMIs occurred between female-female pairs (46.3%,  $n = 69$ ), with the remaining interactions distributed between male-male pairs (28.9%,  $n = 43$ ) and mixed pairs (24.8%,  $n = 37$ ). Therefore, females were involved in the majority of MtMIs, despite both sexes being available for most of those interactions (87.9%,  $n = 131$ ).

### 3.3.3.3 *Same-sex and same-age*

MtMIs between same-sex and same-age partners occurred more often (32.9%,  $n = 49$ ) than between opposite-sex and same-age partners (20.1%,  $n = 30$ ). However, given that same-sex and same-age partners were available more than twice as often as were opposite-sex and same age partners (69.1%,  $n = 103$  versus 32.2%,  $n = 48$ ), the difference is likely due to availability.

### 3.3.4 *Individual differences*

A beluga's age at first participation in MtMIs varied greatly. Some animals were observed initiating MtMIs at 2 months old while others were not observed initiating them until 19 months old (Figure 3.3). To determine if the onset of other social behaviors was correlated with the age of the first MtMI, we used the Kendall correlation test as all behaviors tested (Table 3.3) were non-normally distributed (Shapiro-Wilk  $p < 0.05$ ). The age of onset of MtMIs was only correlated with the age of onset of ventral presents—a socio-sexual display ( $r_{\tau} = 0.58$ ,  $p = 0.04$ )—however, when a Bonferroni correction was applied, none of the other social behaviors, including ventral presents, were significantly correlated. To determine if there were individual differences in the rate of initiating MtMIs, the total number of MtMIs initiated by an individual was divided by the total months

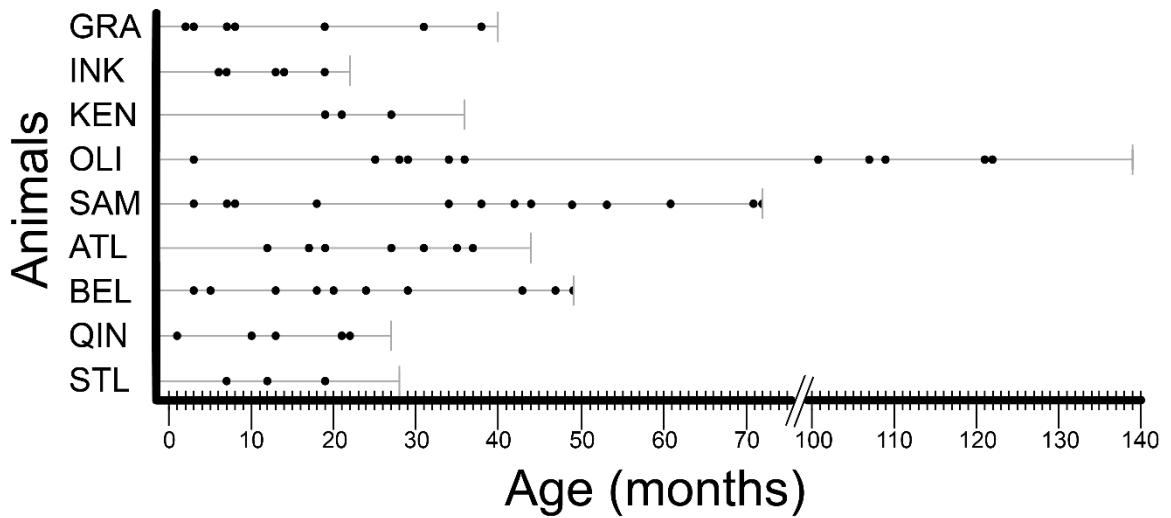
observed. The resulting plot (Figure 3.4) shows that some animals initiated more than double the MtMIs than others (e.g., KEN versus BEL).

**Table 3.3**

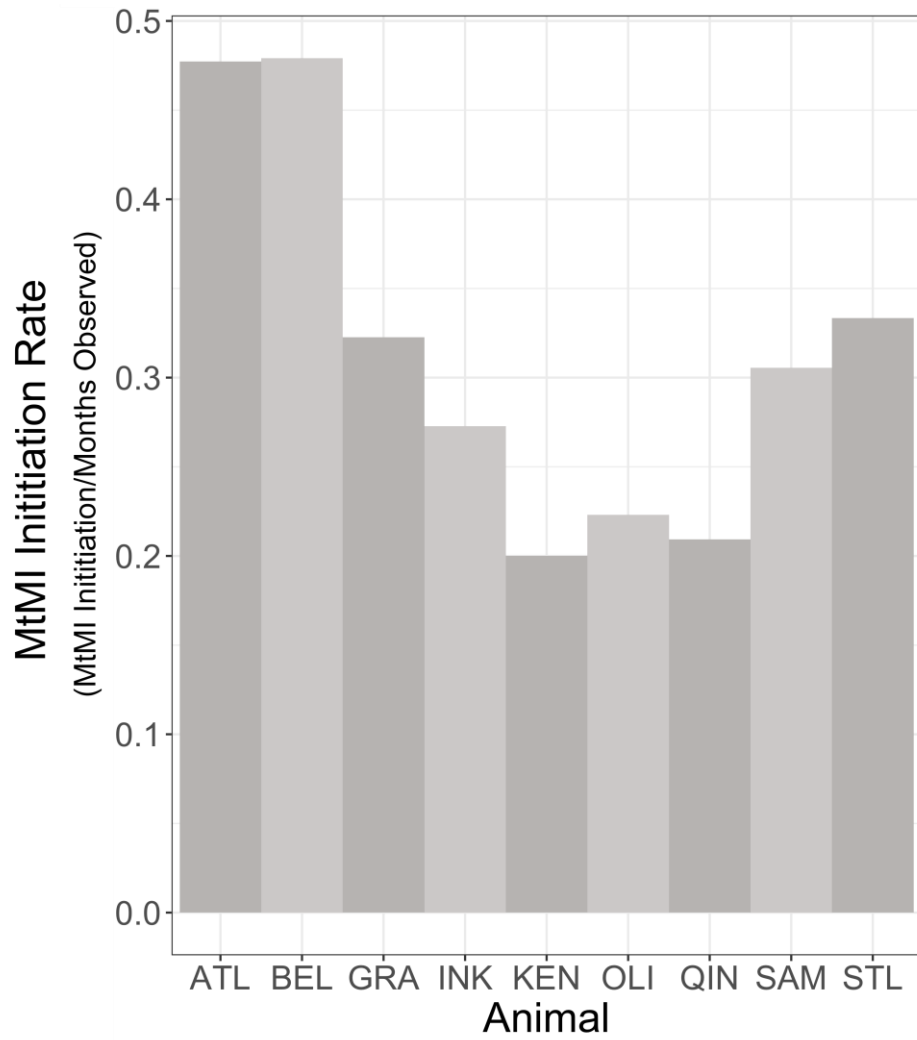
*The age of onset of mouth-to-mouth interactions to predict the age of onset of other social behaviors.*

Factors	Social Category	Test	<i>p</i>
Open Mouth	Aggressive	$r_{\tau} = 0.58$	1.00
Ventral Presents	Sexual	$r_{\tau} = 0.58$	0.28
Pelvic Thrusts	Sexual	$r_{\tau} = -0.21$	1.00
Horizontal S-posture	Sexual	$r_{\tau} = -0.32$	1.00
Genital Rub	Sexual	$r_{\tau} = 0.34$	1.00
Social Play	Affiliative	0.42	0.91
Locomotor Play	N/A	0.30	1.00

Note. \* $p < 0.05$ .



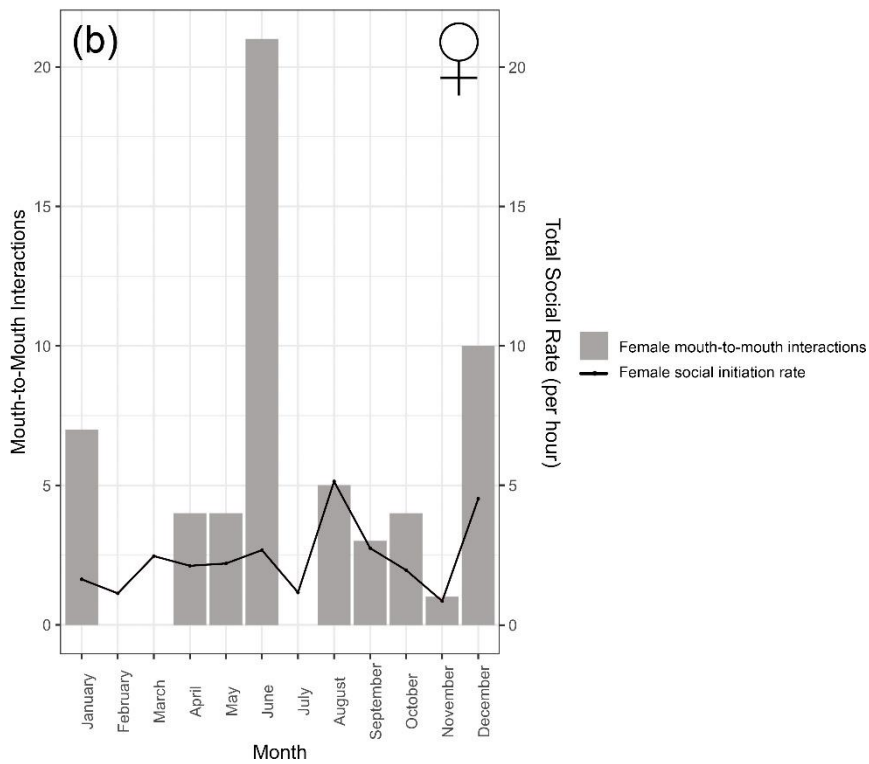
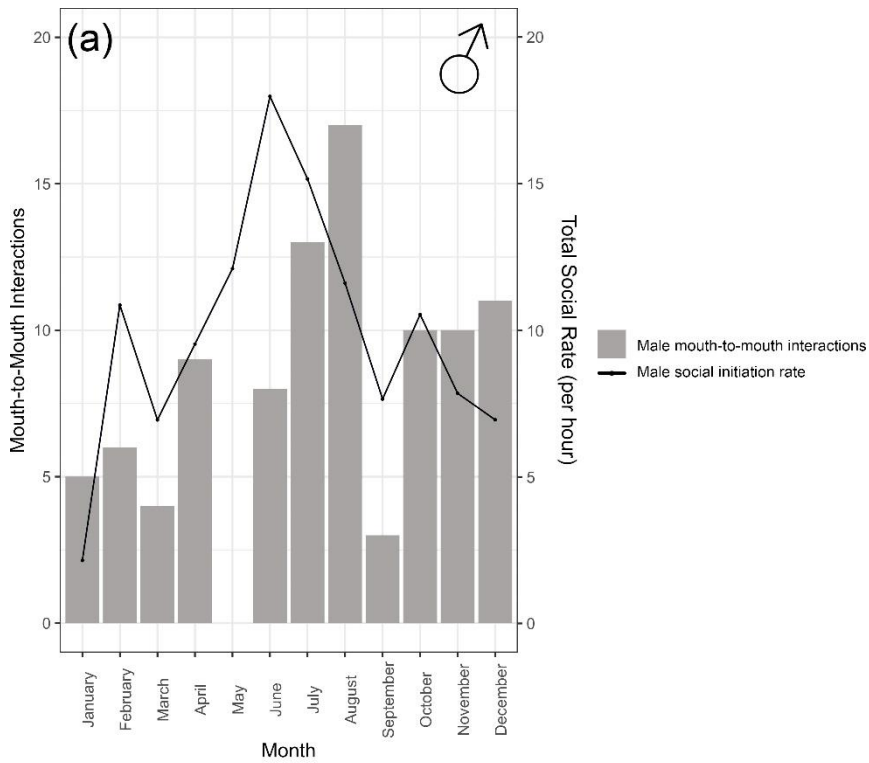
**Figure 3.3** Presence of mouth-to-mouth interactions for each month of life for all 9 calves born at SWoT. This graph illustrates the sporadic nature of these interactions and the variation in the age of onset. The light gray lines reflect the observation period of each animal while the black dots represent the occurrence of mouth-to-mouth interactions (one black dot could be just one MtMI or multiple for any given month of life). Please note that as the animals were born from 2007-2017, this graph does not accurately reflect the conspecifics to which each beluga had access.



**Figure 3.4** A comparison of how many mouth-to-mouth interactions were initiated by each calf when standardized by the number of months they were observed.

### 3.3.5 Seasonality of MtMIs

Initiation of MtMIs was observed year-round, but peaked in the summer (Figure 3.5), with an apparent sex difference as females peaked early in summer (June), and males peaked later (August). To determine if these peaks in MtMIs were an artifact of an overall increase in social behavior, we looked at all other social interactions (socio-sexual, aggressive, affiliative, and play), excluding mother-calf interactions. The initiation of overall social behavior was also seasonal (Figure 3.5). Using the Kendall correlation test, as female MtMIs and sociality were non-normally distributed (Shapiro-Wilk test;  $p < 0.05$ ), we found that the overall sociality of females was not significantly correlated to MtMIs ( $r_{\tau} = 0.35$ ,  $p = 0.125$ ). The same was true for males as shown by a Pearson's correlation test ( $r(10) = 0.26$ ,  $p = 0.407$ ; normally distributed Shapiro-Wilk test;  $p > 0.05$ ).



**Figure 3.5** Both male (a) and female (b) mouth-to-mouth interactions and social frequency as a function of month.

### 3.4 Discussion

Despite MtMIs not being described thoroughly before in any other cetacean species, they have been reported in belugas at several facilities (e.g., Connor and Peterson, 1994; Hill et al., 2019; Recchia, 1994) and in the wild (e.g., Krasnova et al., 2014), suggesting that MtMIs are species-typical. As previously reported for the belugas housed at SWoT (Hill et al., 2019), MtMIs are mostly performed by immature animals, but unlike the earlier preliminary study, we found that MtMIs continue into adulthood, albeit at a much lower frequency. MtMIs emerge within the first few months of life and occur sporadically over the pre-weaning and juvenile periods (Figure 3.3). Our results also show that most MtMIs were initiated by immature animals and most animals partnered in MtMIs were also immature. In contrast, MtMIs involving adults most frequently involved immature animals, and were exclusively initiated by adult males. All nine of the immature belugas studied initiated MtMIs, as did all three adult males. As MtMIs are retained into adulthood, it may be that belugas are employing this social play behavior to test social bonds. Considering that most of the MtMIs by immature animals involved age-matched partners, it might be that, at the earlier ages, this form of social play, like play fighting more generally, is involved in the social and physical development of belugas. In many species, play fighting preferentially involves same-age peers, and often same-sex peers (e.g., Biben, 1986; Cheney, 1978; Koyama, 1985; Meaney and Stewart, 1981; Pellis and Pellis, 2016). By engaging with partners that have only small differences in skill advantage, it has been hypothesized that these interactions provide optimal opportunity for training cognitive and physical skills (e.g., Biben, 1998; Fagen, 1981; Thompson, 1998).

### *3.4.1 MtMIs as social relationship testing*

Although it is unlikely that MtMIs are sufficient in themselves to promote the development of social skills, due to their rarity and sporadic occurrence (making up less than 15% of all social play), they may still provide unique opportunities with which to test social bonds or relationships developed through other types of social interactions (Palagi, 2011; Pellis, 2002). For example, species of Galagidae, small primates known as bush babies or galagos, forage alone at night, but also congregate in small groups before dawn (Aureli et al., 2008). When they congregate, to re-acquaint themselves, they engage in social play (Charles-Dominique, 1978; Clark, 1985). By engaging in social play, animals explore how their own behavior strengthens or weakens their social connections with conspecifics (Kohn, 2019; Pellis, 2002). Belugas may use MtMIs, an unusual form of play, to test social bonds formed through other social interactions (e.g., Lilley et al., 2020), and this could account for retaining this form of play into adulthood.

Further detailed reports on beluga social behavior should continue to consider the emergence of MtMIs and the context in which they emerge to determine if MtMIs are being used to test social relations. For example, in populations in human care, when animals are moved from one facility to another, are MtMIs employed more frequently when the belugas are starting to build new social relationships? In wild populations, do MtMIs peak during summer congregations where animals from varying groups come together in the thousands (Frost and Lowry, 1990; Lydersen et al., 2001; O’Corry-Crowe et al., 2018)? If so, this would lend further evidence that this behavior is used to test social bonds. The seasonal trend in MtMIs, with both males and females peaking in summer months, could also be correlated with the seasonality of reproductive behavior. Not only does mating (Doan and Douglas, 1953; Heide-Jørgensen and Teilmann, 1994; Krasnova et al., 2009; Robeck et al.,

2005; Sheldon et al., 2020) and calving vary seasonally (Sergeant, 1973), but so does socio-sexual behavior and other affiliative behavior (Ham et al., 2021b). This heightened social arousal during the summer months could account for the seasonal trend of MtMIs. This seasonal variation may drive the need to test social relationships in the summer months, especially in adult males.

Unlike the preliminary report of the SWoT belugas (Hill et al., 2019), we found that adult belugas initiate MtMIs. While most of the adult initiated MtMIs were directed toward juveniles (72.7%), all of the adult-adult MtMIs occurred between male pairs. Adult males engage in social behavior frequently, however, it is mostly socio-sexual (Ham et al., 2021b; Hill et al., 2015b). Employing MtMIs to test existing relationships, formed through other social behavior (further discussed below), may be why belugas retain this behavior into adulthood. While adult females do not initiate MtMIs, they are partnered in MtMIs. Interestingly, only one of the mother-calf pairs engaged in MtMIs, with the other adult females partnering with other females' offspring. The variety of partners and the retention of MtMI into adulthood suggests that this behavior may be used to test social bonds in an unusual way.

#### *3.4.2 Dominance, aggression, or an invitation to play?*

Earlier reports suggested that MtMIs may be used to establish dominance relationships (Krasnova et al., 2014). However, close examination of the topography of this behavior does not indicate that there is a 'winner' or 'loser', but rather that MtMIs are a mutually cooperative behavior (Hill et al., 2019). Our current observations of MtMIs suggest that this is a form of social play rather than being related to dominance or aggression, fitting the criteria for play in general (Burghardt, 2005) and play fighting in particular (Smith, 1997). Tactile aggressive behaviors in belugas often result in tooth rakes

on the skin (Ham et al., 2021a). If MtMIs were a form of aggression, then tooth raking, whether teeth are present or not (Stewart, 2012), should occur occasionally. The mouth-lock should be broken by one of the partners who then bites or mouths the other's body. However, this was never observed in any of the instances of MtMIs.

Jaw wrestling or jaw sparring, which looks similar to the MtMIs in belugas, has been described in several species of Carnivora. For example, black bears (*U. americanus*; Burghardt, 1975), coyotes (*Canis latrans*; Fox, 1969), wolves (*C. lupus*; Fox, 1969), and domesticated dogs (*C. familiaris*; Coppinger et al., 1987; Smuts, 2014), have all been described engaging in the mutual interlocking of their jaws during play. In the jaw sparring of dogs, the partners move their heads in such a way as to avoid their teeth contacting the other dog's face, further supporting the view that this is a playful, not aggressive, behavior (Smuts, 2014). Nonetheless, jaw wrestling is rare, with most species orienting toward other body targets during play fighting (Aldis, 1975; Pellis, 1988). One proposed function of this unusual behavior, at least some species, is that it is acting as a play-invitation or play-solicitation (Burghardt, 1975). This is unlikely to account for MtMIs in belugas, as most social play occurs without MtMIs preceding interactions. The scarcity of playful mouth-to-mouth contact in the animal kingdom may be due to the opportunities afforded by body morphology. Species that can manipulate partners with their hands may not only be able to subdue each other manually, but also provide hand-based tactile cues for communication during the encounters (Whishaw et al., 2021).

It may be that in animals like cetaceans that rely more heavily on their mouths to manipulate the world, also use their mouth more in playful contact and thus, social games such as jaw sparring or MtMIs arise (see Llamazares-Martín & Palagi (2021) which photograph California sea lion pups, *Zalophus californianus*, engaging in what looks like

jaw sparring). Although not frequently reported among cetaceans, mouth-to-mouth contact may be widespread. Killer whales engage in affiliative gentle tongue biting, in which two animals face each other making gentle contact with their rostrum, followed by one animal opening its mouth and the other lightly holding its partner's tongue in its teeth (Bain, 1986; Martinez and Klinghammer, 1978; Nakamura and Sakai, 2014; Sánchez–Hernández et al., 2019). Irrawaddy dolphins (*Orcaella brevirostris*), a much smaller euryhaline delphinid, often form groups of individuals that face each other and engage in head-to-head contact after bouts of chasing and mating (see Sutaria et al., 2019). Similarly, bottlenose dolphins will face each other, often with their mouths open, during bouts of socio-sexual behavior and engage in head-to-head contact while emitting vocalizations and blowing bubbles (Connor et al., 2000; Overstrom, 1983). Bottlenose dolphins also engage in mouth-to-rostrum mouthing, in which one animal places its mouth around the rostrum or beak of another (see Hill et al., 2019). In these cases, however, there is no mention of interlocking jaw contact, even though killer whale tongue touching does require the rostrum of one whale to be inside the mouth of the other. A more common form of contact, of many cetacean species, is rubbing. Social rubbing is a form of contact that employs the body and pectoral fin to rub against conspecifics (e.g., Dudzinski et al., 2009; Johnson and Norris, 1994; Mann and Smuts, 1999; Sakai et al., 2006; Smith et al., 1992). Some cetacean species (e.g., belugas, bottlenose dolphins, Irrawaddy dolphins, killer whales) engage in head-to-head or mouth-to-rostrum contact, including MtMIs, as they may provide a different way in which to test social bonds and affiliations than does rubbing. This could explain why these species continue to engage in this contact into adulthood.

### *3.4.3 MtMIs as motor skill development*

MtMIs may also be a way for belugas to train motor skills, as appropriately positioning the body to make mouth-to-mouth contact requires fine motor control. The motor training hypothesis could explain both the early and varied onset of MtMIs. If suitable partners are available with whom to develop social bonds, MtMIs can emerge in their first few months of life (Hill et al., 2016, 2018a). If no suitable partners are available, as shown in the present paper, the onset of MtMIs can be delayed until later in the first or second year of life. However, whether the onset is early or late, MtMIs provide an opportunity for training motor skills.

Consistent with the motor training hypothesis is that most MtMIs involved immature animals (85.7% of those initiated and 90.6% of those received) and most bouts occurred between age-matched partners (71.1%). Indeed, when age-matched partners were available, only 6.5% of MtMIs were observed between non-age-matched partners. Further, while immature belugas of both sexes engaged in MtMIs, female-female partners engaged in more MtMIs than male-male partners (46.3% versus 28.9%). As males engage in more socio-sexual play (Ham et al., 2021b; Hill et al., 2015b; Lilley et al., 2020) than females, females may compensate by engaging in more MtMIs. The same sex preference exhibited by young females engaging in MtMIs may further enhance motor training, as they are playing with partners with a similar level of skill (Biben, 1998; Thompson, 1998). As already noted, MtMIs require as much physical and social coordination as do some of the more complex actions performed during socio-sexual play, so even though MtMIs are less frequent than socio-sexual play (Ham et al., 2021b; Lilley et al., 2020), they may be more beneficial for training purposes.

### **3.5 Conclusions**

Our results indicate that MtMIs are a form of sporadic play behavior, most frequently performed by juveniles. Despite other toothed whales reportedly engaging in head-to-head or mouth-to-mouth interactions, the topography of beluga MtMIs is unique. Further, our findings suggest that immature belugas may engage in MtMIs to train motor and social coordination skills, and both adults and immature animals may use MtMIs to test social bonds. Researchers studying other toothed whales should note the occurrence of head-to-head or mouth-to-mouth interactions, as they may provide insight into the development of social bonds, social skills, and motor skills.

## **CHAPTER 4: DEVELOPING AN ETHOGRAM FOR OBJECT PLAY IN BELUGAS: INSIGHTS INTO BEHAVIORAL SEQUENCES OF OBJECT MANIPULATION**

### **4.1 Introduction**

Object play, a relatively understudied study form of play, is characterized by the manipulation of objects, such as non-human primates engaging in stone handling play (Cangiano and Palagi, 2020; Cenni et al., 2020), horses tossing sticks (McDonnell and Poulin, 2002), or octopuses pushing, pulling, and passing objects from arm to arm (Kuba et al., 2006). Few studies, however, have described the variety and complexity of object play in detail. Species for which detailed studies are available show that object play often structurally resembles other functional behaviors. For example, stone handling in Balinese long-tailed macaques (*M. fascicularis*), is similar to sexual behavior (Cenni et al., 2020) and foraging behavior (Pelletier et al., 2017). Essential for such detailed studies is the development of detailed ethograms of what the animals do during play and during a variety of functional contexts. This approach allows researchers to ask more detailed questions of the behavior they are studying. For example, most of the behavior patterns used in the stone play by long-tailed macaques are derived from the foraging and sexual behavior system (Pelletier et al., 2017), whereas the stone play of geladas (*Theropithecus gelada*) involves behavior patterns not typical of foraging (Cangiano and Palagi, 2020).

Given the variety of foraging habits of marine mammals, this understudied group of mammals offers some novel opportunities to gain insight into what animals do during object play. Some studies report object play in cetaceans (e.g., Cappiello et al., 2018; Delfour et al., 2017; Greene et al., 2011; Ikeda et al., 2018; Soriano Jimenez et al., 2021; von Streit et al., 2013), but an in-depth study that includes a detailed ethogram, is yet to be

provided for any species. Belugas are a toothed whale species that inhabits Arctic waters (O’Corry-Crowe, 2009), that engage in play (e.g., Hill and Ramirez, 2014; Hill et al., 2019), including object play (e.g., Jones and Kuczaj II, 2014; Krasnova et al., 2014). The present study provides a detailed analysis of object play in belugas.

In the wild, belugas play with algae (Krasnova et al., 2014), stones (Armstrong and Mitchell, 2021), and logs (Krasnova et al., 2014). Similarly, in managed care, belugas play with naturally derived objects, such as feathers and leaves, as well as human-made objects that are provided to them as EEDs (e.g., balls, buoys, hula hoop) (Hill and Ramirez, 2014). In both environments, belugas also engage in water play, which is considered to be a form of object play. Water play can involve projecting water streams with the mouth or blowing bubbles either with the mouth or the blowhole. Whether with their mouths or blowholes, they can create singular bubbles (Hill et al., 2011), bubble rings (Delfour and Aulagnier, 1997; Hill and Ramirez, 2014; Hill et al., 2011), and bubble helices (Jones and Kuczaj II, 2014). While water play has received some attention (e.g., Delfour and Aulagnier, 1997; Jones and Kuczaj II, 2014), the broader range of behavior that belugas use during object play has not been described in detail.

This chapter provides a detailed ethogram of the behaviors performed during object play in a population of belugas under managed care. The ethogram was used to quantify the various behaviors and characterize the kinds of objects to which they are directed. Although most bouts of play consisted of a single behavior, some bouts consisted of multiple actions in a sequence. These multi-action sequences were scored using The Observer (by Noldus) in order to analyze whether particular behavior patterns are linked together more frequently than expected by chance. Like the long-tailed macaques (Cenni et al., 2020; Pelletier et al., 2017), it was predicted that the pattern of association in object

play sequences would be correlated with behavior systems from which those behavior patterns are derived. A further goal of the present study was to gain a developmental perspective on object play by comparing the behavior of the immature belugas with that of the adults. Not only does the present study provide new insights into object play, but it also has potential practical value. Play can be used as an indicator of welfare (see Ahloy-Dallaire et al., 2018; Burghardt, 2005; Held and Špinka, 2011), and the data presented here could inform care staff and veterinarians on the use of EEDs in managed care populations.

## **4.2 Methods**

### *4.2.1 Subjects*

The subjects of this study were 19 belugas (immature: 5 males and 4 females; adult: 4 males and 6 females) housed at SWoT. Each subject was housed with several other individuals, including at least one immature beluga within three years of age and with several adult and sub-adult animals. Social groupings of the animals varied daily depending on facility activities and staff decisions.

The animals at SWoT were housed in series of seven interconnected pools that collectively hold approximately 2 million gallons of water. Pacific white-sided dolphins were often housed in adjacent pools to the belugas at any given time.

### *4.2.2 Data collection*






Data were collected via video recordings from 2007 to 2019 at SWoT, using both scan samples and focal follows (Martin and Bateson, 2007). Observations were either from above the water from viewing platforms or through an underwater viewing window. Focal follows were 15 min in length, tracking the behavior of one individual at the time, while scan samples were 20 min in length, scoring the behavior of several individuals at the beginning of each minute. However, if non-focal animals were visible in the focal follow

observations, they were also scored. The collection of data at SWoT was approved by the Institutional Animal Care and Use Committee at St. Mary's University. Observations were made between 0600 h and 1800 h. Videotaping was done when trainers were not present in or near the enclosure. In total, 142 videos were analyzed representing around 38 h of observations.

Following previous studies of object play in bottlenose dolphins (Greene et al., 2011), objects were classified into four categories (Table 4.1): (1) organic/found materials (e.g., feathers, leaves, fish, feces), (2) human-made objects (e.g., buoy balls, cloth mats, hula hoop), (3) water, and (4) environment (e.g., enclosure gate). Human-made objects were provided for the belugas, at random, by the staff of SWoT. It should be noted that not all animals had the same access to all objects, so all human-made objects accessible were noted for each observation.

**Table 4.1**

*Object identification (photographs by H. Hill).*

Name	Type	Example
Ball	Human-made	
Bowl	Human-made	
Bubble burst	Water	
Bubble ring	Water	
Bubble stream	Water	

Buoy

Human-made



Cooler lid

Human-made



Cube

Human-made



Disc

Human-made



Feces

Organic/Found



Flowerpot

Human-made



Funnel

Human-made



Gate

Environment



Hourglass

Human-made



Hula hoop

Human-made



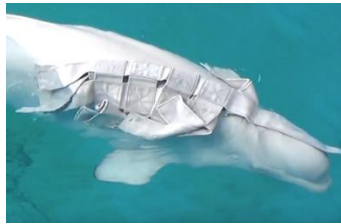
Leaf/twig

Organic



Mat

Human-made



Pipe

Human-made



Rag/towel

Human-made



Rope

Human-made



Seat

Human-made



Small-to-medium bubble

Water



Water spit

Water



#### *4.2.3 Video analysis*

Videos were selected opportunistically from the archived video log, selecting videos that noted “object play,” “EEDs present,” and/or “water play.” All behaviors that occurred with an object (human-made, organic, and the environment) were recorded, along with any water play, noting the behavior, the object manipulated or the type of water manipulation, who initiated the behavior, if the play occurred with a partner (and if so, who the partner was), as well as duration of the behavior. Further, all other play (locomotor and social/sexual) were recorded for its duration, the initiator, the social partner (when applicable), and type of play (e.g., locomotor, social). Information on the age and sex of the subject was also noted.

#### *4.2.4 Sequence analysis*

Play sequences were classified as such if they consisted of three or more play behaviors (including social or locomotor play) occurring within 10 seconds of each other (Berchtold and Sackett, 2007; Izidoro and Le Pendu, 2016; Slooten, 1994). For example, if a beluga tossed a ball, swam for 8 sec without making contact with an object, returned to the ball and mouthed it, and then engaged in social play for 9 sec after mouthing the ball, this would be a sequence. However, if the beluga swam for 11 sec in between tossing and mouthing the ball, this would not be considered a sequence. Further, if the beluga did not engage in social play at the end of the sequence (i.e., the beluga only engage in two play behaviors: toss and mouth), this would also not be a sequence. Using these criteria, 328 videos were scored that included independent behavioral sequences representing around 4.5 h of observations. In order to score these behavioral events in more detail (i.e., sequential analysis), each behavior sequence was extracted from the original 15 – 20 min scan sample and focal follow video by trimming the original observations to just include

the behavior sequence. If multiple behavior sequences occurred within one 15 – 20 min observation, the video would be trimmed multiple times so that each sequence was captured in a shortened clip. The individually trimmed video sequences were then scored using The Observer XT 12 (by Noldus).

Object play behaviors (Appendix C) were scored as non-mutually exclusive, as some behaviors overlapped (e.g., beaching and carrying an object). Behaviors such as beach, push down, push forward, toss, and carry could also be scored with mouthing behavior as a modifier (although animals could engage in each of those behaviors without the modifier). When animals were not engaging in object play, they were scored as either engaging in social play, motor play, or swimming (further broken down into solo-swim or social-swim), all of which were scored as mutually exclusive behaviors.

Although some play does serve immediate functions (e.g., Palagi et al., 2006), it is often less structured than non-playful functional behaviors, such as those involved in foraging (e.g., Burghardt, 2005; Hughes, 1978, 1979; Rasa, 1984). Therefore, the first prediction was that play is unconstrained and so sequences are likely to be random (e.g., Cenni et al., 2020). Alternatively, object play sequences may be stereotyped or fixed and are not malleable. It is also possible that certain classifications of whales are more unconstrained than others (e.g., immature individuals versus adults). To determine if the sequences were stereotyped or random, lag-sequential analysis was used. For current purposes, only lag-1 transitions were analyzed—that is, transitions that occur between pairs of behavioral elements. Lag-sequential analysis is way to measure sequential dependency on preceding behaviors. By analyzing lag-1, the first behavioral dependency is evaluated. In other words, it evaluates the likelihood that the second behavior follows the first behavior in a sequence. Furthermore, behavior patterns that are functionally and causally linked,

such as those associated with sex or with foraging, were clustered into presumptive behavior systems (Hogan, 1994; Timberlake, 1993; Tinbergen, 1951), following the method used for categorizing stone-handling play in macaques (Pelletier et al., 2017). Thus, the behavior patterns used in the object play of belugas were categorized as *system* (the overarching behavior system: feeding, social, and motor behaviors), *mode* (sub-categories of behavior systems: communication, forage, and predation), and *action* (the actual behavior expressed, for example: bite/mouth, toss, and water spit).

#### 4.2.5 Statistical analysis

Single action play with objects was plotted using bubble plots to illustrate, for each beluga, both the behaviors (Figure 4.1) and the objects (Figure 4.3) used. Bubble plots visually demonstrate the differences among the individual percent of play as well as between age groups. Similarly, sequences of object play were plotted using bubble plots to illustrate, for each beluga, both the behaviors (Figure 4.4) and the objects (Figure 4.6) used. To determine if animals engaged in some behaviors more often than others and used some objects more frequently than others, Kruskal Wallis tests were used as all data were determined to be non-normally distributed (Shapiro Wilks  $p < 0.05$ ). A post-hoc Dunn test, with a Bonferroni correction, was used when tests were significant using the package *FSA* (Ogle et al., 2021) in R (R Core Team, 2020).

To illustrate differences in the use of object type (i.e., environment, human-made, organic, and water), a graph was made using *ggplot* (Wickham, 2016). In order to illustrate pair-wise associations between behaviors, sequence diagrams were created for the behaviors that followed each other at least 20 times. While other associations between behaviors were significant, using a minimum of 20 times occurrence ensures that the illustrated sequences are both frequent and significant. These data were then examined

using Chi-square tests to see if they were correlated to a behavior system. Immature and adult animals were analyzed separately so as to ensure that age-related comparisons could be conducted.

### 4.3 Results

#### 4.3.1 Object play ethogram: Single action object play

A total of 17 behavioral patterns were identified and described (Appendix C). It should be noted that, while the descriptions are written as if the belugas engage in only one behavior with one object at a time, they can engage with multiple objects simultaneously. Video clips illustrating the items in the ethogram listed in Appendix C can be found at: <https://youtu.be/Lh2Ycss9q5Q>

Out of the 19 subjects studied, only one subject, an adult male, did not engage in object play. Because observation times for each individual varied, the rate of single action object play was calculated by dividing the total number of bouts by the total time scored (Table 4.2). This rate, however, does not represent the daily rate of object play as the videos scored here were specifically scored for occurrence of object play. Nonetheless, the data can be used to assess individual differences, showing that belugas in the sample engaged in significantly different rates of object play (Kruskal-Wallis test:  $H(1) = 10.14, p = 0.001$ ). Further, when separated into immature and adult belugas, immature whales engaged in significantly more object play than adults ( $p = 0.0007$ ), after a Bonferroni correction. No significant difference was found between male and female engagement in object play ( $H(1) = 0.44, p = 0.51$ ).

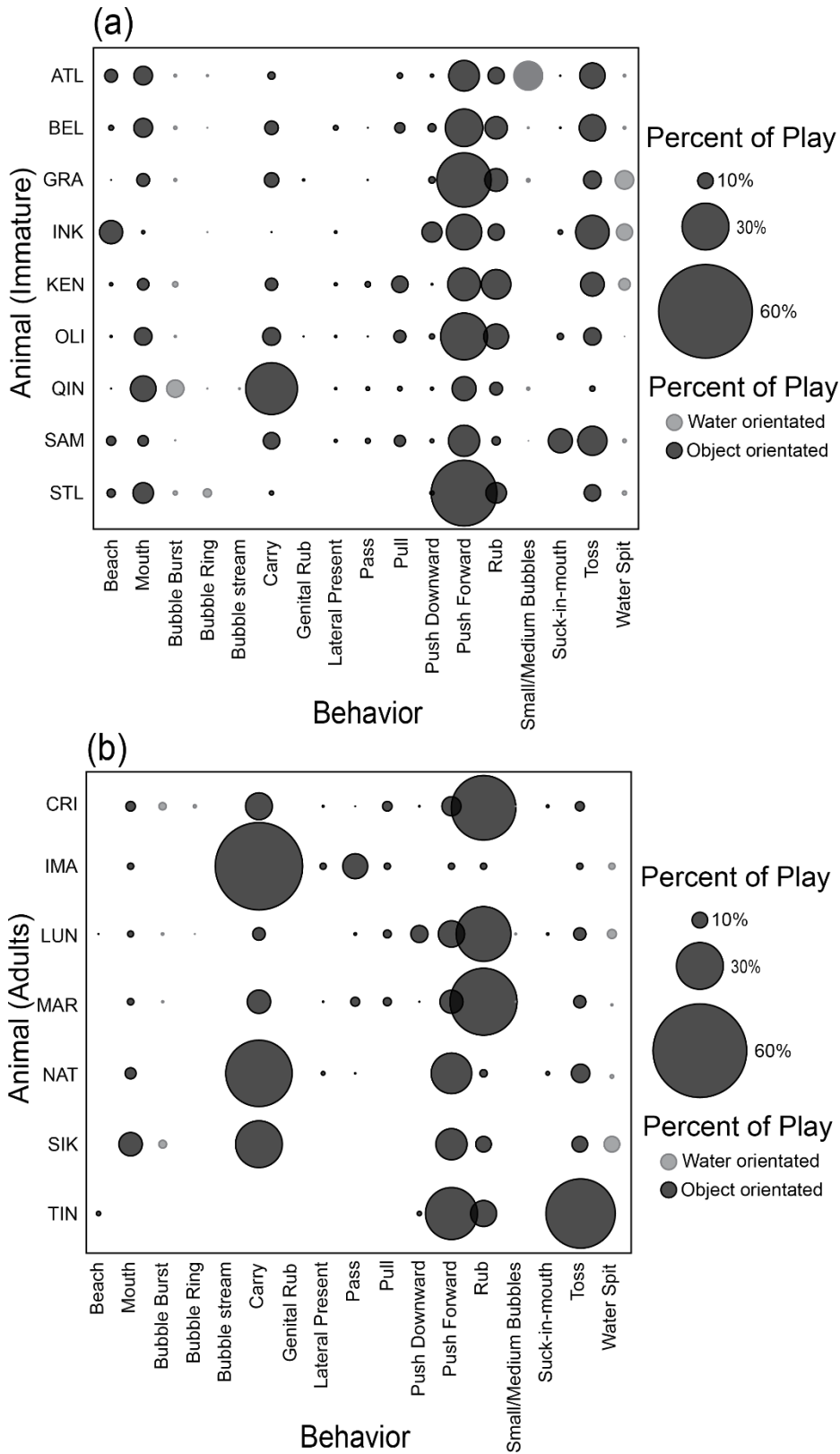
**Table 4.2***Summary of single action object play behaviors for each animal.*

Animal	Number of object play bouts	Total time scored (hour:min)	Rate of object play standardized for observation time (bouts/hour)	Average duration of play bout (seconds)
ATL	294	6:47	43.32	3.76±3.68
BEL	886	8:10	108.52	7.51±11.57
BET	8	0:15	31.96	20.38±17.06
CRI	178	21:29	8.28	7.42±9.28
GRA	246	6:52	35.88	8.33±22.31
IMA	25	12:14	2.04	5.00±3.77
INK	242	4:24	55.04	5.07±6.63
KEN	201	7:38	26.36	5.82±6.89
LUN	431	20:54	20.62	8.93±14.17
MAR	291	19:28	14.94	6.90±7.37
NAL	1	1:03	0.95	2.00
NAT	50	11:32	4.34	7.59±9.35
OLI	816	23:03	35.40	10.75±17.69
QIN	208	4:27	46.72	11.19±16.24
SAM	352	14:25	24.42	8.77±9.99
SIK	20	4:27	4.49	25.79±26.96
STL	38	4:37	8.24	15.41±16.92
TIN	36	4:30	8.01	8.87±8.58
WHI	0	0:46	0	0
Average			25.23	8.91±10.97

The duration of single action object play was variable, averaging  $8.91 \pm 10.97$  sec (Table 4.2). Because some individuals were observed more than others, the time sampled was standardized to 4.5 h. Animals observed for less than 4 h were removed from further analyses (i.e., BET, NAL, and WHI) and animals with more than 5 h were subsampled to limit the time sampled to 4.5 h. The subsampling selected videos that involved human-made objects, so as to ensure that all such objects were scored at least once. This was done because certain objects afford opportunities for different behaviors (e.g., suck-in-mouth cannot occur with an object such as a buoy ball, as it is larger than the beluga's mouth, but can with a leaf). The standardization was based on human-made objects because these were introduced randomly by the animal caretakers, whereas the animals always had access to the physical environment and water. Access to organic objects, like feathers, were randomly available, and so were not able to be tracked systematically. The 4.5 h of video was randomly subsampled three times for each individual, with any object interaction meeting the above criterion being included. The three sub-samples were then compared to the total observation time available for each animal, to ensure that this sampling was a reliable way to standardize our data. A Chi-square test was used to compare the proportion of behaviors between subsamples and full samples. For example, OLI was observed for a total of 23 h, in which he engaged in push forward 25% of the time. Similarly, in the 4.5 h sub-sample, OLI also engaged in push forward around 25% of the time. For most individuals, there were no significant differences, and for animals that did differ significantly, this was limited to only one or two behaviors, and this difference in proportion only varied by 3-5%. Thus, the randomly sampled 4.5 h data set was an accurate representation of the behaviors. As such, the results presented below are based on the subsampled, 4.5 h standardized data.

### 4.3.2 *Single action behaviors*

Both immature (Figure 4.1a) and adult whales (Figure 4.1b) engaged in single action object play behaviors at significantly different frequencies ( $H(16) = 102.22$ ,  $p < 0.0001$  and  $H(16) = 72.406$ ,  $p < 0.0001$ , respectively). As seen in Figure 4.1, while immature belugas frequently engaged in all 17 behaviors, adults tended to use only a few of the available behaviors. Further, post-hoc Dunn tests, with Bonferroni corrections, showed that, for immature whales, ‘push forward’ was performed more often than any other behavior, whereas, for adults, there were no significant pairwise comparisons.

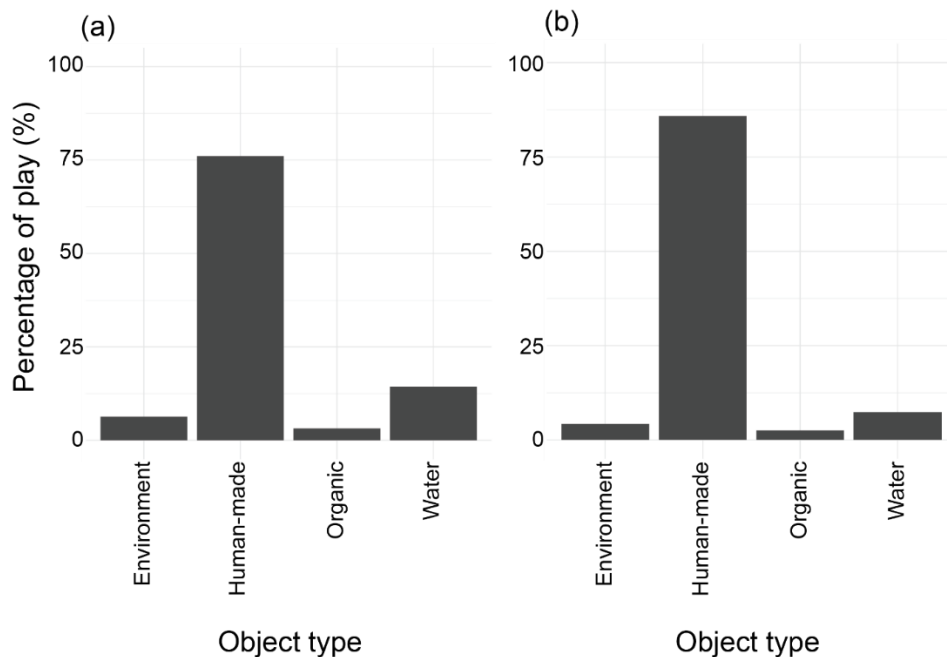


**Figure 4.1** The percentage of each behavior used in single action object play for both immature (a) and adult (b) belugas.

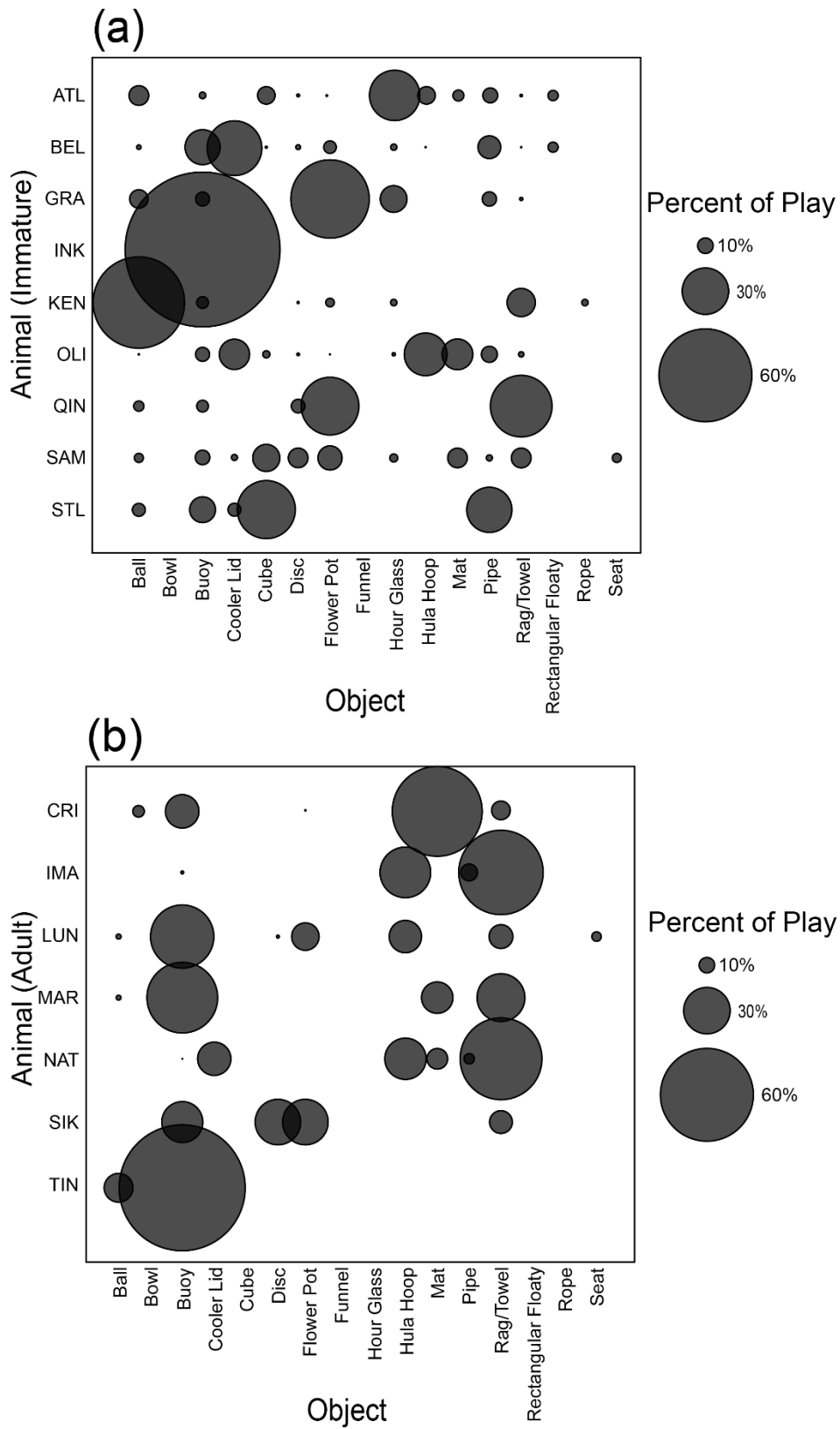
### 4.3.3 Single action play with objects

Human-made objects were the most frequently used objects by both immature (Figure 4.2a) and adult belugas (Figure 4.2b), making up 76.1% and 85.8% of their object play, respectively.

Both immature and adult whales used specific human-made objects at significantly different frequencies ( $H(15) = 52.10$ ,  $p < 0.0001$  and  $H(15) = 50.431$ ,  $p < 0.0001$ , respectively). Post-hoc Dunn tests, with Bonferroni corrections, revealed that both adults and immature animals used buoy balls more often than other objects. As well as buoy balls, immature whales used other types of balls more frequently. Immature animals tended to manipulate a wider variety of objects than adults (Figure 4.3).



**Figure 4.2** The percentage of play employing each object type for both immature (a) and adult (b) animals.



**Figure 4.3** The percentage that each object was used in single action object play for both immature (a) and adult (b) belugas.

#### *4.3.4 Behavioral sequences*

Of the 19 animals observed in this study, 16 engaged in sequences of object play. The shortest sequence was 7 sec, while the longest sequence was 6 min 38 sec, with an average length of 52 sec (Table 4.3). The shortest sequence, meeting our definition, was 3 behaviors, while the longest involved a string of 76 behaviors. No sequence incorporated all 17 of behaviors in the ethogram (Appendix C), and the maximum number of different types of behavior in a sequence was 12.

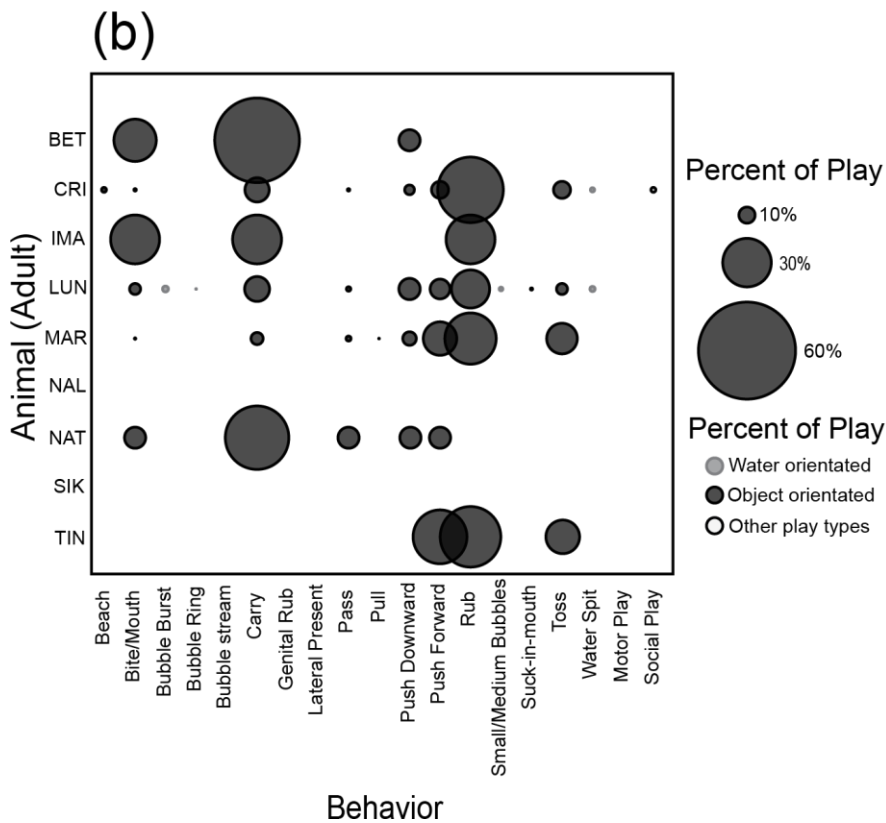
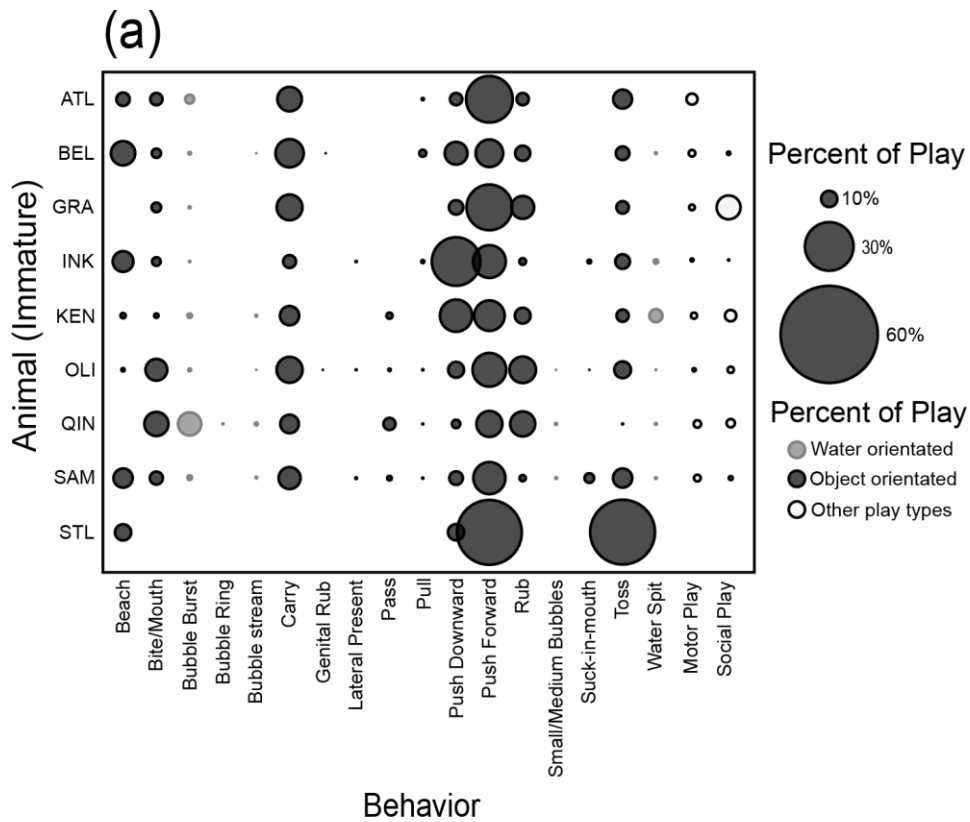
**Table 4.3***Summary of sequenced object play behaviors for each animal.*

Animal	Number of sequences scored	Total time scored engaging in sequential play behavior (min:sec)	Average sequence length (min:sec)	Average number of behaviors in sequence*	Average number of different behaviors in sequence†
ATL	20	11:23	00:34	7.30±4.69	3.45±1.47
BEL	56	60:32	01:05	13.20±14.15	4.54±2.15
BET	1	01:42	01:42	7.00	3.00
CRI	4	07:53	01:58	15.25±11.84	4.25±0.83
GRA	23	16:35	00:43	7.39±4.21	4.04±1.16
IMA	1	00:09	00:09	3.00	3.00
INK	15	18:46	01:10	16.69±21.15	4.25±1.95
KEN	18	13:20	00:44	10.33±8.83	4.50±1.54
LUN	28	25:36	00:55	7.18±6.07	3.32±1.17
MAR	29	20:25	00:42	7.17±3.18	3.38±0.76
NAL	0	-	-	-	-
NAT	5	03:04	00:37	4.20±1.47	3.40±1.02
OLI	75	57:19	00:46	7.36±5.17	4.01±1.29
QIN	14	15:55	01:08	12.50±13.11	4.86±2.07
SAM	34	24:22	00:43	8.41±7.49	4.12±1.39
SIK	0	-	-	-	-
STL	2	00:58	00:29	5.00	3.00±1.00
TIN	3	02:03	00:41	7.33±1.70	3.00±0.00
WHI	0	-	-	-	-
Total	228	278:09	00:52	8.71±7.93	3.76±1.27

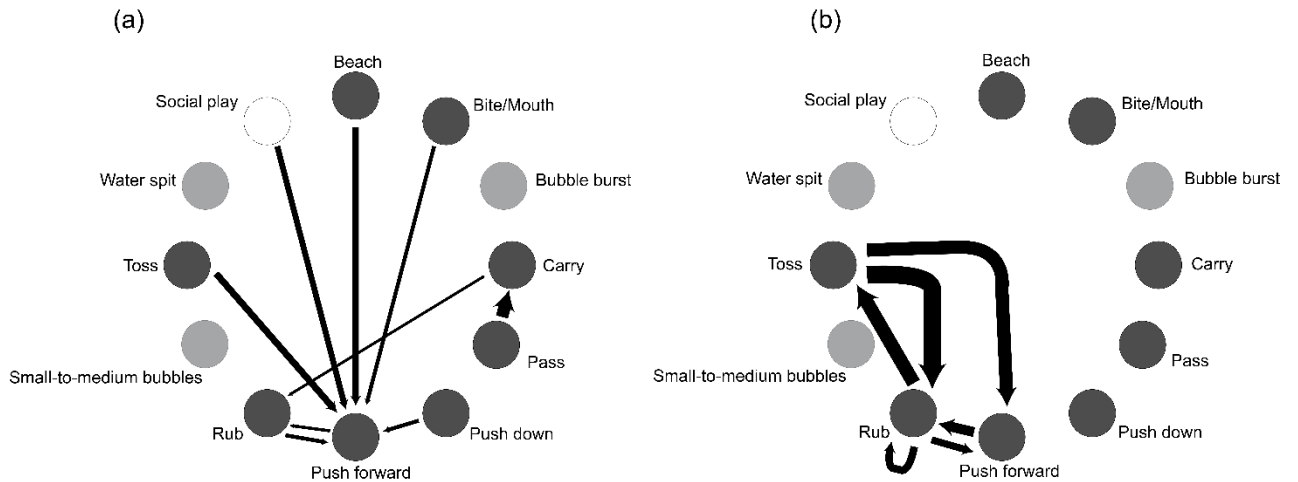
\*This does not include non-play, swimming behaviors (i.e., solo-swim or social-swim). It does include repeated behaviors (e.g., carry → pass → carry → toss → social swim → carry = 5 behaviors sequential behaviors); †not including non-play, swimming behaviors (i.e., solo-swim or social-swim) and does not include repeated behaviors (e.g., carry → pass → carry → toss → social swim → carry = 3 unique different sequential behaviors).

#### *4.3.4.1 Behavior of object play sequences*

Both immature (Figure 4.4a) and adult whales (Figure 4.4b) engaged in specific behaviors in sequences at significantly different frequencies ( $H(18) = 109.18, p < 0.0001$  and  $H(18) = 67.50, p < 0.0001$ , respectively). Post-hoc Dunn tests, with Bonferroni corrections, revealed that immature animals engage in more bite/mouthing, pushing downward, and pushing forward than most of the other types of play behavior, while for adults only carrying occurred more than other behaviors.



**Figure 4.4** The percentage that each behavior was used in object play sequences for both immature (a) and adult (b) belugas.



**Figure 4.5** Sequence diagrams for both immature (a) and adult (b) belugas. Each node represents a specific behavior and the thickness of the arrows indicates the proportion of the time a given behavior is followed by another. Note that this illustrates the most frequent, and significant, lag-1 sequences.

Sequential behaviors were more varied in immature animals than adults (Figure 4.5). For example, immature belugas beach before pushing objects forward 17.7% of the time, but also engaged in social play (16.7%), tossing (19.0%), and biting/mouthing (11.14%) before pushing objects forward. In contrast, adults rubbed 50.8% of the time after tossing objects and also pushed objects forward 37.3% after tossing objects. After rubbing, adults tossed objects 38.9% of the time. By only using the most frequently occurring behaviors in sequences, that occurred at least 20 times, it is clear that the play behaviors of immature whales were more flexibly linked together than was the case for adults.

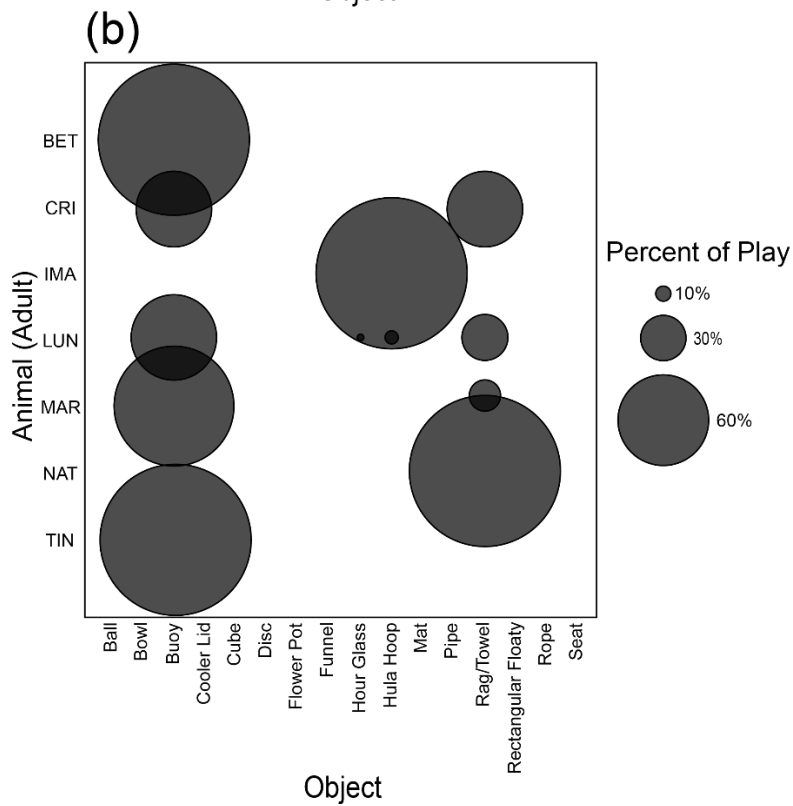
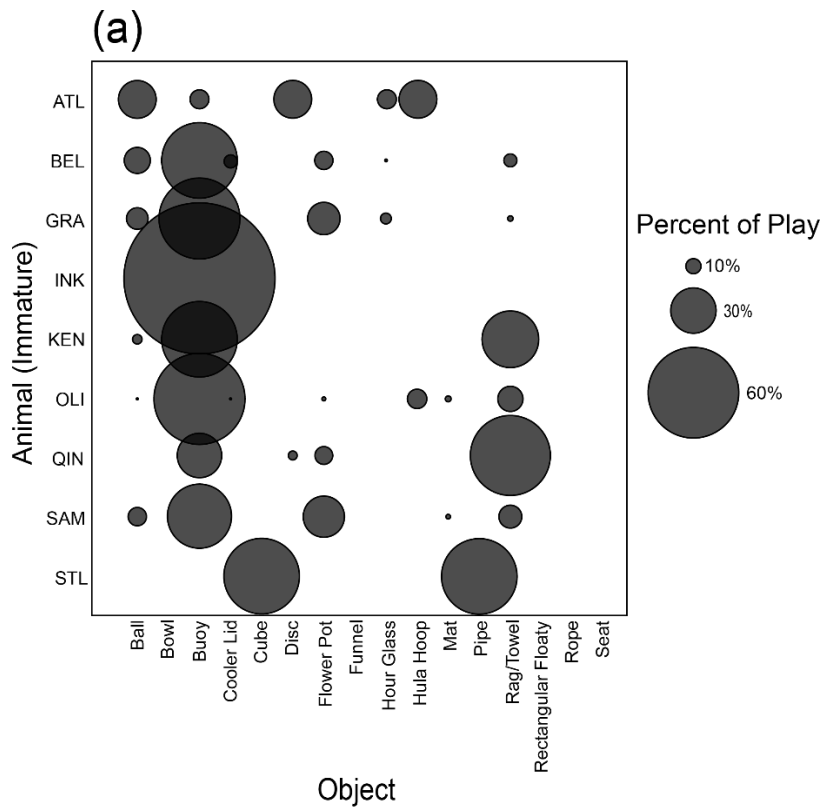
#### 4.3.4.2 Objects used in object play sequences

Both immature (Figure 4.6a) and adult (Figure 4.6b) whales engaged with specific human-made objects at significantly different frequencies ( $H(16) = 55.82, p < 0.0001$  and  $H(16) = 57.74, p < 0.0001$ , respectively). Post-hoc Dunn tests, with Bonferroni corrections, revealed that both immature and adult whales used buoy balls more than other types of

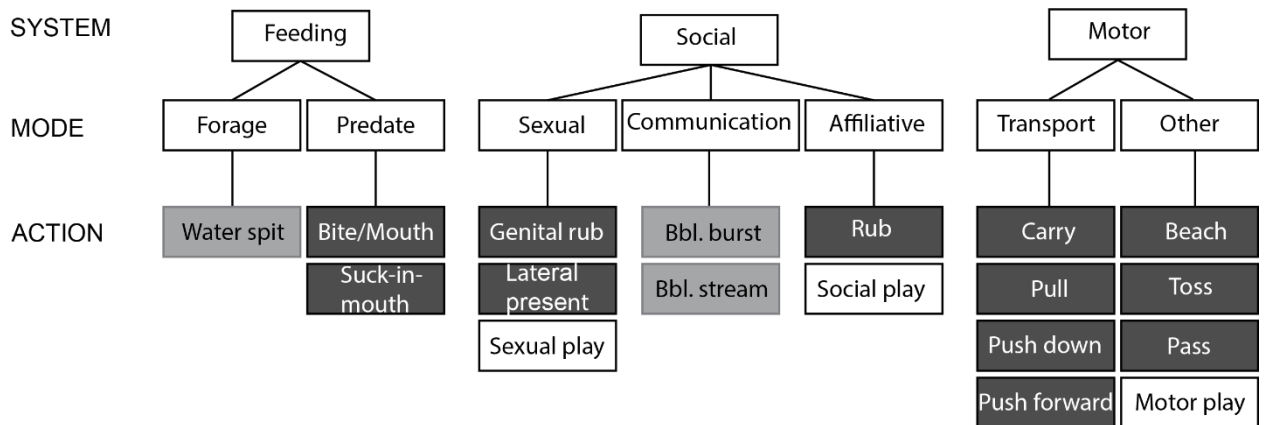
objects. Although the overall use of objects in sequences was more limited than object play not involving sequences (compare Figures 4.2 and 4.6), immature animals played with a wider variety of objects than adults did in both cases.

#### *4.3.4.3 Sequential object play and behavior systems*

Most of the behavior patterns (actions) occurring in sequences could be categorized into three behavior systems and seven modes (Figure 4.7), with a few, such as bubble rings and small-to-medium bubbles, not able to be categorized. A Chi-square test was conducted to determine if behaviors within one system (e.g., bite/mouth, water spit, and suck-in-mouth; 'feeding' *system*) occurred more frequently together, in sequence, than by chance. For both immature and adult animals, no significant association was found between behaviors in a behavior system. These findings suggest that actions from different behavior systems are randomly combined during object play.



**Figure 4.6** The percentage that each object was used in object play sequences for both immature (a) and adult (b) belugas.



**Figure 4.7** Behavior systems diagram representing the various behaviors or “actions” described in the ethogram (Appendix C). Note that bubble ring and small-to-medium bubbles have been excluded as they did not fit a behavior system.

## 4.4 Discussion

### 4.4.1 Ethogram behaviors

As with most types of play, immature animals engage in more object play than adults (Auersperg et al., 2015; Gamble & Cristol, 2002; Hill & Ramirez, 2014; Nahallage & Huffman, 2007; O'Hara & Auersperg, 2017), and, as shown in the present study, this is also true for object play in beluga whales. However, not only did immature animals engage in more object play than adults, but it was also more variable. This was true for both the range of behaviors performed, the variety of objects used and the variability of the sequences. Adult sequences were more stereotyped and predictable; this suggests that there might be a shift to more stereotypical play with age. One explanation for this greater flexibility in the immature animals may be that object play is being used by them as practice for adult behaviors.

It has been suggested that young animals use object play to practice foraging behaviors (Gamble and Cristol, 2002; Kuczaj and Eskelinen, 2014; Pellis et al., 2019b). If this is the case, immature animals should engage in more varied play in order to maximize their opportunities to practice these behaviors in novel contexts. Once adult, it is unlikely that they would need to continue to practice behaviors and so, would instead limit their play to what they find rewarding. However, detailed studies on object play in belugas are required to see if immature animals that engage in frequent object play improve their foraging skills as adults. Also, this hypothesis does not account for why both immature and adult whales seem to randomly intermix actions derived from social and motor/swimming behaviors with actions derived from foraging behavior. Since, in actual foraging, it is unlikely that animals engage in sexual behavior with the prey, intermixing such actions during object play would seem antithetical to practicing foraging skills. Also unexplained

by this hypothesis is why there is so much inter-individual variation in which behavior patterns are performed during object play.

Although 17 distinct behaviors could be used during object play (Appendix C), not all animals engaged in all 17 behaviors. In part, this may be due to variation in access to objects as different objects afford different opportunities to use distinct play behaviors. The objects presented to belugas at SWoT were mostly buoyant; the belugas were able to push objects below the surface of the water, which often lead to objects quickly accelerating back to the surface when the animal stopped pushing on the object. Thus, while buoyant objects may differentially stimulate behaviors such as ‘push down’, objects that remain submerged or float below the surface, such as rags, stimulate other behaviors, such as ‘carry’. It is possible that a wider range of available objects could expand the ethogram beyond that used in the present study. Further, bubble helices, as described by Jones and Kuczaj II (2014), were never observed by our animals; this difference cannot be explained by access to objects, but rather, may reflect population differences. By extension, it is possible that the repertoire of behaviors used in object play by the SWoT population may not represent the full repertoire for this species. Irrespective of variation across populations and the opportunities afforded by different objects, the present study shows that even when the same objects are available to all, different individuals prefer to engage with certain ones. This suggests that individual differences need to be considered when studying object play.

A limitation of ethograms, such as the one used here, is that even specific behaviors are described in a generalized manner. For example, “toss” is defined as ‘to move or throw an object upwards out of the water’ (Appendix C), but the way in which belugas can toss an object is highly variable (see video ethogram). Belugas can toss an object by biting it

and flicking it, holding it on their tail flukes and quickly propelling it into the air, or by just pushing an object out of the water quickly with their melon or head. That is, while the ethogram item of tossing has a common component - the object is propelled into the air - how this is achieved can be highly varied. If such variation is scored, much higher levels of inter-animal variation may become apparent, not only potentially revealing a high degree of creativity in object play (Dudzinski et al., 2018), but also further lessening the explanatory value of the practice hypothesis.

Nonetheless, given the limited knowledge of object play in beluga whales, the present ethogram provides a starting point to begin such a program of study. For example, bottlenose dolphins (Cappiello et al., 2018; Ikeda et al., 2018; Soriano Jimenez et al., 2021; von Streit et al., 2013) incorporate more motor play (e.g., jumping and flipping) when playing with objects. However, while the frequency likely differs, behaviors such as mouthing and rubbing will likely be found universally throughout odontocete object play.

Further research on object play in belugas should also investigate social object play. Although not nearly as frequent as solo object play, belugas were observed engaging in social, and potentially even cooperative play, with objects. One form of social play, is 'keep away', in which one beluga tries to steal an object from another, as has been described in several mammal species (Burghardt et al., 2016; Pellis, 1991; Shimada, 2012; Tanner and Byrne, 2010), and may be important for developing and maintaining flexible problem solving skills (Kuczaj et al., 2006).

#### *4.4.2 Sequential analysis*

The sequential analysis provided here revealed that object play in belugas can be very complex. Although infrequent, some sequences were more than 12 behaviors long, with the longest sequence consisting of 76 consecutive play behaviors. Even though both

immature and adult belugas engaged in object play involving sequences of several distinct behaviors, the sequences by immature animals were more complex and varied than that of adults. Adult behavior was rather stereotypical, often consisting of push forward → rub → push forward. As suggested above, these age-related differences may relate to immature animals using object play to practice future adult behaviors and/or to develop and maintain problem solving skills, although the mixing of behavior patterns from different behavior systems would seem to diminish the value of object play as practice.

One way to understand behavior is to examine which behavior patterns are correlated, indicating that they are elements of a ‘behavior system’; that is, a cluster of behavioral elements that are functionally and causally linked in a hierarchical manner (Tinbergen, 1951). For example, the foraging behavior system in Balinese long-tailed macaques is composed of modes of behavior such as food searching, food investigation, and food processing. In turn, food searching involves collecting food objects and to do so, they use behavior patterns such as grasping and holding to pick up food items. Object play in this species involves using behavior patterns within the foraging behavior system (Pelletier et al., 2017).

By categorizing the behavior systems from which the behavior patterns in the beluga object play ethogram is composed (Figure 4.7), I was able to explore whether behavior patterns derived from the same behavior system were more likely to occur in the same sequence. They are not. Rather, in both immature and adult belugas, behavioral elements from distinct behavior systems (e.g., foraging, social communication) were combined together in sequences of object play (Figure 4.5). These results suggest that belugas are able to ‘mix’ behavior patterns from a number of different behavior systems, and so disconnect specific behavior patterns from the functional sequences from which they

are derived (Pellis et al., 2019b). However, this conclusion may be unwarranted due to the assumptions upon which the lag sequential analyses were based.

For example, based on other studies involving sequence analysis of behavior in odontocetes (e.g., Izidoro and Le Pendu, 2016; Slooten, 1994), I chose behaviors occurring within 10 seconds of one another as constituting components of the same sequence. However, 10 seconds may be too long or too short to encompass a meaningful sequence of behavior in belugas. That is, if this time frame was too short, we may be missing other behaviors that would make sequences more complicated. In contrast, if the time frame chosen was too long, the seeming combination of behavior patterns from multiple behavior systems may be an inaccurate portrayal of how the behavior is linked together. Belugas are a slow-moving species and so require lots of time to reposition themselves, so it remains to be determined if 10 seconds is an appropriate time frame to distinguish the beginning and end of behavioral sequences.

The sequence analyses strongly indicate that the behavior of immature animals is more varied and complex than that of adults. This developmental change suggests that the framework for sequence analysis used in this study may be ethologically meaningful. Future analyses involving the behaviors that occur third (i.e., lag-2) and fourth (i.e., lag-3) in the sequence may provide further insight into how behavior patterns are combined. If behavior patterns from different behavior systems are linked together in longer sequences that would further support that the framework can accurately reflect the organization of object play in belugas. Linking long strings of behavior patterns from multiple behavior systems would suggest that, like dolphins (Dudzinski et al., 2018), belugas are creative in their play.

## **4.5 Conclusion**

By developing an ethogram of object play in belugas, a framework is provided with which to gain a better study of beluga play behavior. Belugas of all ages made use of their structural environment, including the surrounding water, human-made objects and naturally occurring organic objects, and engage in a variety of complex behaviors during object directed play. The human-made objects provided were the most frequently played with types of objects. As such, facilities housing belugas should continue to provide human-made objects or EEDs, as these objects likely improve welfare and enhance the animal's quality of life (Kuczaj et al., 2002).

## **CHAPTER 5: GENERAL DISCUSSION**

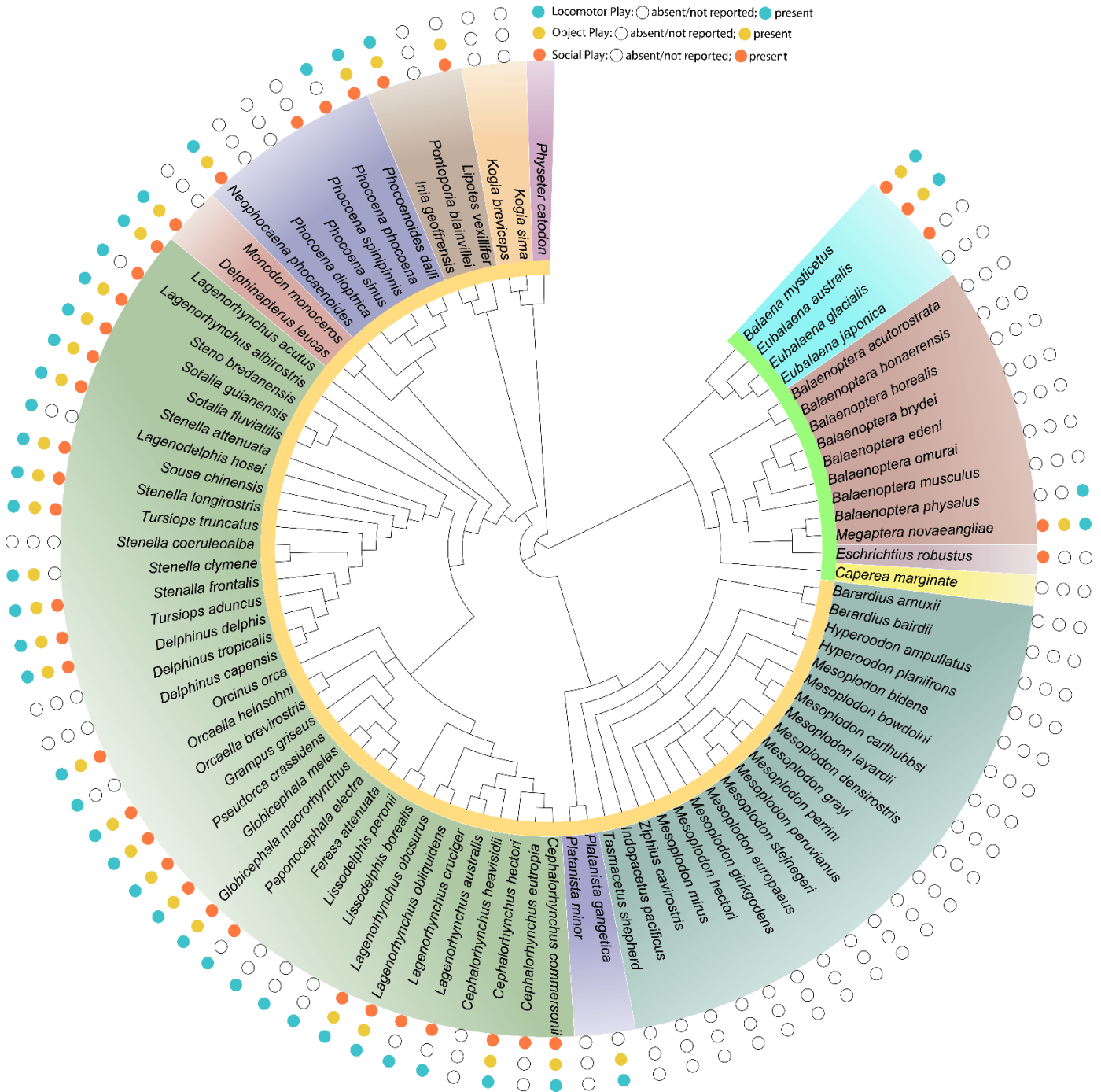
The play of belugas is diverse, including social play, object play, and locomotor play (Hill and Ramirez, 2014; Hill, 2009). This thesis provides descriptive analyses of two forms of social play (sexual play and mouth-to-mouth interactions, Chapter 2 and Chapter 3, respectively) and object play (Chapter 4). Locomotor play, a common form of play in Cetacea (Paulos et al., 2010; Würsig, 2009), remains to be described in detail in belugas. Often proposed as being comparable to some non-human primate species (Furuichi et al., 2014; Nakamura and Sakai, 2014), dolphins and whales provide a convergent clade with species having relatively large brains (Hof et al., 2005) to compare and contrast play.

### **5.1 Species comparison**

The play of belugas is similar to that of other cetaceans (Paulos et al., 2010), especially toothed whales. For example, both killer whales and bottlenose dolphins engage in mouth-to-mouth contact (e.g., Martinez and Klinghammer, 1978; Overstrom, 1983; Sánchez–Hernández et al., 2019), sexual play (e.g., Ford, 2009; Mann, 2006; Martinez and Klinghammer, 1978), and object play (e.g., Delfour et al., 2017; Guarino et al., 2017; Kuczaj II and Yeater, 2006; Martinez and Klinghammer, 1978; McCowan et al., 2000; Pace, 2000). Play is also present in some species of baleen whales as well, being reported to engage in sexual play (e.g., Parks et al., 2007; Sironi, 2004) and object play (Owen, 2012; Würsig, 1988; Würsig et al., 1989). A comparative survey shows that all forms of play are widely distributed in the order (Figure 5.1). Given how few species have been studied in detail, the many instances of absence of play in the cladogram likely reflects absence of evidence, rather than being truly absent. Clearly, further research is needed, but the wide occurrence of play across the clade and its considerable complexity in some of the

species in this lineage does appear to make Cetacea an important order for comparison with primates.

A feature that identifies species as having complex social play is the presence of interspecies play (Chevalier-Skolnikoff, 1990; Maglieri et al., 2020; Maple and Zucker, 1978). Many species of whales and dolphins engage in interspecific play (e.g., Deakos et al., 2010; Herzing and Elliser, 2013; Ikeda et al., 2018; O’Callaghan and Massett, 2020). For example, humpback whales lift bottlenose dolphins out of the water on their rostrum (Deakos et al., 2010). Importantly, while being lifted out of the water, the dolphin appears to cooperate with the whale by arching its body in order to remain balanced on the whale’s rostrum, suggesting a high degree of coordination and communication between the two species. While not the focus of the present study, our belugas were observed to play with the Pacific white-sided dolphins that they were housed with on several occasions. For example, the belugas engaged the dolphins in sexual play and playful chases. The diverse social systems (Fox et al., 2017) and variation in brain size (Marino et al., 2004, 2007; Montgomery et al., 2013) in Cetacea offers the opportunity to identify the socio-cognitive skills that are needed for complex interspecies play to emerge.



**Figure 5.1** A cladogram describing which species of Cetacea engage in social (orange), object (yellow), and locomotor play (blue). The cladogram was built using 10K tree project data (Arnold et al., 2010) and was constructed using FigTree.

Comparison of closely related species, but with divergent morphologies, may also prove useful in understanding the organization of play. The closest relative of belugas, the narwhal (*Monodon monoceros*), has received little research attention due to its remote Arctic habit. Indeed, in some rare instances, it seems that belugas and narwhals group together and though very rare, there is evidence that narwhals and belugas can reproduce (Skovrind et al., 2019). As they have a similar body size and shape to belugas, I would suspect their play would also be similar. However, mouth-to-mouth interactions would most likely be impossible or made greatly difficult due to their large tusk, especially in adults. If mouth-to-mouth interactions are important, as they seem to be in belugas and some other species of toothed whales (Chapter 4), it is likely that narwhals may have developed an alternative form of social play to compensate. Alternatively, playful interactions could employ their tusk, in a similar manner to that suggested for aggressive behavior (Gerson and Hickie, 1985), or beluga-like mouth-to-mouth interactions could be restricted to juveniles before the tusk is grown. Due to their similarities (e.g., habitat, size, social structure) and their differences (e.g., tusk), comparing the play of belugas and narwhals could provide insights into the functions of play.

## **5.2 Why do belugas play? One theory does not fit all!**

Many hypotheses about the function of play have been proposed, such as the practice hypothesis (Groos, 1898), the motor-training hypothesis (Bekoff and Byers, 1981), and training for the unexpected hypothesis (Špinka et al., 2001). These hypotheses concern the delayed functions of play – play as a juvenile, benefit as an adult (Fagen, 1981) - and have been applied to all forms of play (i.e., locomotor, object, and social play) and to any species that engages in such behavior. However, the evidence can be contradictory. For example, testing the hypothesis that play fighting, a type of social play, is used to train

combat skills (Groos, 1898; Smith, 1982) across species has been supported for some species (e.g., Blumstein et al., 2013), but not others (e.g., Sharpe, 2005). Also, many species continue to engage in play fighting (Pellis and Iwaniuk, 1999, 2000), or other forms of play, such as stone play in macaques (Nahallage et al., 2016), into adulthood, at which age the play has immediate, not delayed, functions. There are likely many functions of play, some delayed and some immediate, which may apply in a particular case depending on the type of play performed (e.g., Pellis and Pellis, 2017), the species (e.g., Pellis, 1993), the age of the player (e.g., Palagi et al., 2004), and potentially even the sex of the player (e.g., Pellis et al., 1997). Certain aspects of beluga play described in this thesis are consistent with some proposed functions of play while others are not.

The two forms of social play studied in this thesis, sexual play and mouth-to-mouth play, may be thought of as just two variations of ‘social play’, and since both are most frequent in the juvenile period, may be considered to provide a similar delayed function (e.g., motor-training hypothesis; Bekoff and Byers, 1981; training for the unexpected; Špinka et al., 2001). However, some features of these two forms of play suggest that they may have distinct functions, even when performed by juveniles. For sexual play, the preferred partners are older males, whereas for mouth-to-mouth interactions, the preferred partners are same age animals—and same sex if you are an immature female beluga. Since for optimal motor skill training partners should only differ a little in skill level, the best play partners should be close in age (Thompson, 1998). That being the case, mouth-to-mouth interactions are more likely to be of benefit for motor training. Making the encounters more challenging (e.g., Barrett et al., 2021; Petrů, et al., 2009), as would likely be the case for juveniles playing with older males, makes sexual play more consistent as a means for training for the unexpected. Alternatively, the different partner preferences may

reflect two different ways in which social relationships are tested and maintained (Pellis and Iwaniuk, 2000). By playing with same age partners, animals may be developing long-term bonds, whereas by playing with older animals, the initiators may be using play to climb in the dominance rank of the pod (e.g., Mills, 1990). Thus, while both mouth-to-mouth interactions and sexual play are a form of social play, they may be used for different immediate and delayed functions. Herein lies the problem with applying specific hypotheses too generally. While hypotheses may be applicable to certain aspects of play, they are not necessarily applicable to all forms of play (i.e., locomotor, object, social play), or, as shown here, even within a seeming single category (e.g., social play). Such multiple uses may be common, even if the specific functions may differ from species to species.

Killer whales that inhabit the coastal waters of British Columbia, Canada, engage in vigorous sexual play (Baird, 2000). While such play has been thought to provide practice for sexual skills, sexual play occurs is at its most frequent when pods congregate in the spring months (Baird and Dill, 1995; Rose, 1992). When pods first come together, groups of immature killer whales form and start engaging in vigorous sexual play. This yearly burst of sexual play has been hypothesized to be a way for the animals to greet one another and become reacquainted (Rose, 1992).

Much like comparing specific types of play among species, caution must be used when comparing the function of a given type of play at different ages. For example, while immature and adult belugas employ the same behavior patterns during object play, the organization differs markedly. Immature animals use a greater variety of behavior patterns and engage with a greater variety of objects. In contrast, sequences of object play by adults are more stereotyped and their interactions are limited to fewer types of objects. If object

play is beneficial, it is unlikely that the same function will account for the play of immature and adult belugas.

One common explanation for object play in immature animals is that play with objects practices foraging techniques (Gamble and Cristol, 2002; Kuczaj and Eskelinen, 2014; Pellis et al., 2019b), thus, object play is serving a delayed benefit. However, adults, who do not need to practice adult behaviors, also engage in object play. In adults, playing with objects may be therapeutic, preventing age-related cognitive decline (Nahallage et al., 2016). Thus, while the behaviors may appear similar, the functions may differ markedly depending on the age of the player. Indeed, the flexibility and variation observed in the object play of immature belugas suggests that young belugas may also be using object play to create unpredictable situations, and so train for the unexpected (Špinka et al., 2001).

This lesson, that hypotheses to explain the functions of play do not explain *all* forms of play, or even the same type of play, such as social play, needs to be used when trying to compare play across species. While belugas make interesting subjects, due to their relatively large brain (Hof et al., 2005), complex social structure (O’Corry-Crowe et al., 2020), and playful disposition (Hill and Ramirez, 2014), the major conclusions of this thesis, with regards to play behavior, is that caution must be used when making general claims of even a single form of play (e.g., sexual play). In species that engage in a variety of forms of play (e.g., beluga social play consists of sexual play, MtMIs, cooperative object play, etc.), detailed analyses of all types of play must be conducted, before drawing general conclusions on the basis of a detailed analysis of one type of play. The generalization may not be universally applicable.

### 5.3 Future directions

The present thesis provides detailed descriptions of several types of play in belugas, which, in turn, has provided some novel insights into the potential functions of play. In addition, new, and unexpected, avenues for further research have been identified. While Chapter 4 focuses on solo play with objects, it became apparent that belugas also engage in social play with objects, that involves considerable cooperation between partners. I also noticed an interesting phenomenon—self-handicapping during object play. Objects can be used to self-handicap during locomotor play (Petrů et al., 2009) and social play (Pellis and Pellis, 2009), but to my knowledge, self-handicapping during object play itself has not been documented. This observation opens the possibility that, under some situations, object play can be used to train for the unexpected (Špinka et al, 2001), a function not typical associated with this form of play. As I showed for social play (Chapters 2 and 3), object play may not be one unitary activity with one function. Different play experiences may provide unique opportunities for specific functions. Some functions, such as using play to burn excess energy and so regulate metabolic activity (Barber, 1991), not only provides an immediate benefit, but is agnostic on the content of play – all that matters is whether playful behavior is rigorous enough to shed excess calories. In contrast, some proposed functions, such as training for the unexpected (Špinka et al., 2001), not only require that a certain amount of play is performed, but that that play must include specific experiences, in this case, the loss of control that arises from self-handicapping (Pellis et al., 2010). For species with a rich repertoire of play, such as belugas, much more research is needed to explore the full range of possible functions of different forms of play. Indeed, locomotor play, aspects of which can be incorporated in both social and object play, has been little studied in belugas. Who knows what insights may arise from a detailed study of this type of play may yield, but

based on my experience with social and object play, I would guess is that this could be another rich avenue of research to pursue.

Another factor for future studies to consider is the possibility that, in such large-brained and long-lived species as the beluga, cultural variations in play may arise in particular populations, as has been shown for stone play in macaques (Nahallage et al., 2016). Wild belugas likely do not play as much as those housed in managed care, but the type of play in which they engage seems similar (e.g., Krasnova et al., 2014; O’Corry-Crowe et al., 2020). Nonetheless, while the broad categories of play may be similar across populations, it cannot be assumed that the specific variations in the various types of play studied in the SWoT population are the same in all populations. Cultural variation may reflect non-functional variation or adaptation to local conditions, as may be case for nut cracking in wild chimpanzees (Boesch et al., 1994). Not only are detailed studies across multiple populations of the same species needed to determine if there are commonly applicable functions for particular kinds of play, but also other species of cetaceans need to be studied at a similar level of detail to determine if species living with similar social and physical challenges have converged on comparable styles of play.

## CHAPTER 6: REFERENCES

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**APPENDIX A: OPERATIONAL DEFINITIONS OF SEXUAL PLAY BEHAVIORS**

<b>Type of Social Interaction</b>	
Socio-sexual	Interaction in which actor displays any one of the behaviors described by Hill et al. (2015b) to be central to the socio-sexual repertoire. Open mouth behaviors alone were not scored as socio-sexual unless directed at the genital region of the recipient.
Agonistic	Interaction in which the actor chases, bites, head jerks, or directs its open mouth at a recipient and displays no other socio-sexual behaviors.
Affiliative	Interactions that are not socio-sexual or agonistic in nature. This includes pairs swimming together and cooperative play with EEDs.
<b>Behavioral components and actions</b>	
Open mouth	The actor, while facing another animal, rapidly opens its mouth fully and holds it open for at least 1 second. Mutual open mouths can occur.
Mouthing	The actor opens its mouth and rubs it along the receiver's body, but does not leave rake marks The actor may also gently place its mouth on the receiver's flukes.
Mouth-to-mouth interactions <sup>†</sup>	Two belugas face each other and make mouth to mouth contact. This involves mutual coordination and collaboration.
Bite	The actor visibly places its mouth on the recipient and leaves tooth rake marks.
Head jerk	The actor makes a quick head movement toward a recipient
Chase	Actor swims rapidly towards a recipient, while the recipient swims away from the actor.
Riding/surfing	One animal rides on the back of another; this usually occurs at the surface of the water. This can be paired with a gentle rub. This, similar to herding (i.e., one animal directing the swim pattern of another with their body, often done by the

	mother towards her calf) or pelvic thrusting.
Lateral swim	The actor rotates its body so that its pectoral fins are pointed toward the surface.
Side present	The actor positions its body parallel to the receiver's body and presents its ventrum.  At young ages, this is often incorporated into motor play (slapping its pectoral fins on the water's surface while presenting - a behavior rarely observed in adults).
Pectoral fin up	The actor extends its pectoral fin away from its body so that its fin is perpendicular to its body.
Genital rub	The actor moves its genital region along a receiver's body or an object.
Erection	The actor extends its penis externally from its genital slit.
Horizontal s-posture	The actor positions its body in a lateral swim position with its genitalia thrust forward, while the rest of its body adopts a curved posture with its flukes held back. It holds this position statically, for 2-3s.
Vertical s-posture	The actor positions its body vertically in the water column in the shape of an S, and holds it there, statically, for 2-3s.
Pelvic thrust/Mounting	The actor pushes its genital region toward a recipient.
Intromission	The actor inserts its penis into the genital slit of either a female or male.

*Note.* Adapted from Hill et al. (2015b); †Hill et al. (2019).

## APPENDIX B: OPERATIONAL DEFINITIONS OF MOUTH-TO-MOUTH INTERACTION BEHAVIORS

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Behaviors	
Mouth-to-mouth interaction (MtMI)	Two individuals gently clasp each other's mouth and then pull in opposite directions (i.e., like a handshake but with the mouth).
Social behavior	Including socio-sexual behavior (an actor displays sexual posturing, thrusts, penile erections, see Hill et al. (2015b)), affiliative behavior (social swims and play), and agonistic behavior (an actor chases, bites another, as well as head jerks, or open mouths at another). For the purposes of this paper, we excluded mother-calf interactions from overall social behavior.

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*Note.* Adapted from Hill et al. (2019) and Lilley et al. (2020).

## **APPENDIX C: ETHOGRAM OF 17 OBJECT PLAY PATTERNS PERFORMED BY BELUGAS AT SEAWORLD OF TEXAS**

### Object specific:

**Beaching:** To swim onto a platform in shallow water where most of the body is out of the water.

Comment: The animal often employs this behavior when an object gets stuck within its environment and so requires its retrieval. This behavior might be followed by a bite once the animal has beached and can reach the object in order to remove it from there.

**Bite/Mouth:** The animal approaches an object and grasps it with its teeth.

Comment: This behavior is often used by the animal to manipulate the object further by biting the object and then carrying or pushing it in its mouth. This behavior can also be done with water bubbles (Delfour & Aulagnier, 1997). This behavior is often used when “pulling” an object.

**Carry:** The animal holds or balances an object on its own body while swimming/moving.

Comment: The animal may carry an object with its pectoral fins, tail flukes, or by resting and/or balancing the object on its body while swimming. This is often performed with towels, mats, or rags that are light, flexible, and easy to ‘drape’ around the fin. This behavior can precede or follow a “pass” behavior.

**Genital rub:** The animal makes contact with an object using its genitalia.

Comment: Genital rubs might include penile erections. This behavior could include pelvic thrusts in which the animal, in addition to making genital-object contact, pushes its genital region toward an object (Hill et al., 2015b). This behavior is different from a “rub”, as a “genital rub” does include sexual posturing. This rubbing behavior is also done in such a way so that the animal only rubs its genitals rather than a large portion of its ventral side.

**Lateral present:** The animal rotates its body so that one of its pectoral fins is pointed towards the surface and the ventral side of its body is directed towards an object and held there, statically, for 2-3s (adapted from Hill et al., 2015b).

Comment: This behavior can either be with or without posturing, meaning that this also include s-posture presents, in which the animal positions itself either vertically or horizontally within the water column and forms a position in which the animal pushes its genitalia forward and bends its tail flukes back, forming an ‘s’ shape with its body and is held there, statically, for 2-3s Hill et al., 2015b).

Pass: The animal moves an object from one part of its body to another.

Comment: This behavior is often characterized by the animal moving an object (e.g., a mat or a towel) from a pectoral fin to its tail flukes (i.e., the animal ‘carries’ the object on a pectoral fin and then releases it, while continuing to swim, and then catches it and ‘carries’ it with its tail flukes). This, however, is different from “carry” as it is the action of moving the object from one part of the body to another.

Pull: The animal moves an object while swimming backwards.

Comment: This behavior is often performed by the animal when it is “biting” the object.

Push down: The animal moves an object down the water column.

Comment: This behavior allows the animal to move/manipulate an object down into the water. When an animal pushes an object down the water column, this might be achieved by slapping the object with its chin and then swimming over the top of the object so as to keep it below the surface of the water. The animal might also jump or attempt to surf on the object, which pushes the object down into the water. Often the animal will attempt to keep its body over top of the object so keeping the object underwater.

Push forward: The animal moves an object by advancing it forward in the water.

Comment: This behavior allows the animal to move/manipulate an object by moving it forward. This is often done with its rostrum or head. The animal pushes an object forward as it swims.

Rub: The animal swims by an object while making contact with the object with any part of its body but without sexual posturing.

Comment: This behavior could involve the animal swimming past an object and rubbing its entire body length on the object or just a small portion of its body. The dorsal, ventral or sides of its body might be used to contact the object. The animal might also trap an object between itself and a wall and rub itself along the object. Occasionally, while rubbing against an object that is in between its body and the wall, the beluga will lift the object out of the water and hold it elevated above the water (up to around 25 cm above the water’s surface) for a few seconds to around ten seconds.

Suck-in-mouth: The animal sucks an object into its mouth.

Comment: The animal performs this behavior with small objects that can fit in its mouth (e.g., feathers, feces, fish). This behavior is also done with water bubbles (Delfour & Aulagnier, 1997). This behavior is often repeated in quick succession with the animal sucking and pushing the object in and out repeatedly.

Toss: The animal moves or throws an object upwards, out of the water.

Comment: This behavior can be performed by the animal pushing an object out of the water with its rostrum/head, by flicking it with its tail flukes, or by biting it and then throwing the object up into the air.

Water specific actions:

Bubble burst: The animal releases a large amount of air below the surface of the water. This creates a visible ripple on the surface of the water. This release of air is not accompanied by respiration at the surface of the water. (Adapted from Hill et al., 2011; McCowan et al., 2000).

Comment: This large exhalation of air underwater creates many bubbles. Animals have been observed blowing bubbles below objects, which causes the objects floating on the surface of the water to move.

Bubble ring: The animal forms a bubble in the shape of a doughnut (adapted from Hill et al., 2011; McCowan et al., 2000).

Comment: Bubble rings may be formed and ignored, or they may be further manipulated by the animal (e.g., orienting at them as they move, biting at the bubbles).

Bubble stream: The animal releases a continuous stream of small bubbles while swimming forward, creating a trail of bubbles (adapted from Hill et al., 2011; McCowan et al., 2000).

Comment: Bubbles could be further manipulated by the animal by biting them, swimming through the bubbles, or interacting with the bubbles with their rostrum.

Small-to-medium bubble: The animal releases a single bubble (adapted from Hill et al., 2011; McCowan et al., 2000).

Comment: Bubbles could be further manipulated by the animal by biting them or interacting with the bubbles with their rostrum.

Water spit: The animal ejects water through its mouth in a concentrated stream.

Comment: This behavior is derived from the foraging repertoire and can be directed at the surface of the water, conspecifics, or at objects. In some instances, the animal spits the water into the mouth of another conspecific (who catches the water) in a form of cooperative social play. Irrawaddy dolphins have also been reported to spit water at a conspecifics body (Sutaria et al., 2019).