

The Frequency of Contact in Beluga (*Delphinapterus leucas*) Calf Social Interactions

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Abstract

The frequency of contact in the development and maintenance of beluga calf social bonds was examined using video footage collected between 2007 to 2012 for five mother–calf pairs in managed care. Mothers and calves spent ~48% of their time together over a 2-y period, and calves initiated ~45% of their shared social interactions during their time together. Across both years, calves initiated 98% of contact events with their mothers and were in contact over 30% of their time together (i.e., 1.6 contact events/min during an interaction). Contact between calves occurred ~9% of calf–calf time, which was very similar to the time calves spent in affiliative interactions with their mothers outside of mother–calf swims. These results indicate that contact may be particularly important to the development and maintenance of mother–calf bonds and calf–calf bonds during a beluga's first 2 y of life.

Key Words: beluga, *Delphinapterus leucas*, bonding, contact, social interactions, calf, tactile interactions, white whale

Introduction

Social bonds are critical to the survival and welfare of social species (e.g., Silk et al., 2003; Foster et al., 2012) and have been argued as the catalyst for evolving more complex brains (Dunbar & Schultz, 2007). Socially complex societies as displayed by elephants (*Elephas* sp.), killer whales (*Orcinus orca*), and baboons (*Papio cynocephalus*) rely on strong associations between related and unrelated conspecifics to keep offspring safe and the group robust (elephants: Payne, 2003; Plotnik & de Waal, 2014; killer whales: Foster et al., 2012; baboons: Silk et al., 2003). The

creation and maintenance of social bonds with conspecifics incorporates a broad range of behaviors, including proximity, synchronized movements, vocal interactions, and physical contact. Physical contact has multiple functions in social bonds: to develop mother–offspring bonds; to strengthen alliances, especially for submissive animals; and to mitigate agonistic interactions (in elephants: Lee & Moss, 1986; in primates: Schino, 2001; Silk et al., 2003; Dunbar, 2010).

Cetaceans, especially many delphinids, form bonds like other socially complex species that are characterized by synchrony in swimming and breathing patterns, close inter-animal proximity, and physical contact (Dudzinski, 1998; Gubbins et al., 1999; Miles & Herzog, 2003; Connor et al., 2006; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017). Affiliative physical contact occurs relatively frequently between delphinid conspecifics and mother–calf pairs and typically involves various fin and body contact (Herman & Tavolga, 1980; Dudzinski, 1998; Mann & Smuts, 1999; Connor et al., 2006; Sakai et al., 2006; Tamaki et al., 2006; Kaplan & Connor, 2007; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017).

Physical contact between delphinids has been assessed most frequently for adult animals (Dudzinski, 1998; Connor et al., 2006; Sakai et al., 2006; Tamaki et al., 2006; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017). In particular, pectoral fin contact has been studied the most with results suggesting that it is used to develop and strengthen bonds between conspecifics and is similar in form and frequency across populations, including animals in managed care or their natural habitat (Dudzinski, 1998; Connor et al., 2006; Sakai et al., 2006; Tamaki et al., 2006; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017). Less research has focused on the role of physical contact between mothers and their calves.

Physical contact between mothers and their calves may serve two functions: (1) meeting the survival needs of the calf directly (i.e., nursing, providing safe refuge, resting opportunities, and protection against threats) and (2) building a bond (i.e., attachment).

Survival Function

Nursing and discipline are two contexts in which contact can occur within mother–calf pairs or calves with allomaternal caretakers (Reid et al., 1995; Mann & Smuts, 1999; Krasnova et al., 2006, 2009, 2014; Hill et al., 2007, 2013; Hill, 2009; Leung et al., 2010). Nursing can only occur during the infant swim position in which a calf is positioned below the mother's peduncle with its melon or rostrum in alignment with the mammary slits (Figure 1). Previous research has established that melon-to-mammary contact during infant position facilitates nursing while also providing energy conservation to the calf and protection from predators (Weihs, 2004; Noren et al., 2006, 2008; Lyamin et al., 2008; Noren & Edwards, 2011). Additionally, the infant position likely provides contact comfort to the calf and maybe to the mother and may facilitate observations of models engaged in different types of behavior for the calf (Herman & Tavolga, 1980; Gubbins et al., 1999; Mann & Smuts, 1999). In delphinids, the pattern of contact and use of infant position does not decrease linearly as the infant matures but, rather, increases from the first year to the second year (Mann, 1997).

Bond Formation Function

Newborn Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) initiate nearly all of their contact using different types of body rubs, which has been described as “the most common form of newborn socializing, beginning in the first days of life with the mother” (Mann & Smuts, 1999, p. 548). In juvenile delphinids, this rubbing behavior continues between individuals of different sexes, although a sex preference for a preferred partner seems to emerge during this period, duplicating what will ultimately be observed to occur between adults (Kaplan & Connor, 2007). These types of affiliative physical contact do not occur during infant position; instead, they occur during pair swims and other affiliative social interactions.

Despite this knowledge about the nature of physical contact in some delphinids, a systematic investigation of the nature and potential function of physical contact in the development of social bonds has not been established for calves of other odontocetes. The purpose of the current study was to begin to explore the function of tactile contact between belugas (*Delphinapterus leucas*). Beluga

mother–calf pairs exhibit the same types of swim positions and similar maternal care and calf behaviors as delphinids (Krasnova et al., 2006, 2009, 2014; Hill, 2009; Hill et al., 2013; Hill & Campbell, 2014). Research on beluga mother–calf pairs in the Russian White Sea indicated that mothers and calves form strong associations with each other during the first year of life that were characterized by close contact swimming in either echelon position (calf positioned near the mother's dorsal ridge) or infant position (Krasnova et al., 2006, 2009, 2014). Beluga calves often show very early behavioral independence (e.g., increased distances from mothers and frequent independent swims) despite a period of dependence that lasts 2 to 3 y until nutritional independence (Krasnova et al., 2014). These same developmental trends have been confirmed in a population of belugas in managed care (Hill, 2009; Leung et al., 2010; Hill et al., 2013; Hill & Campbell, 2014). Unfortunately, few studies have followed the behavioral and social development of calves beyond the development of the mother–calf bond during the first year of life.

The primary objective of the current study was to quantify the development of social contact in beluga calves. As the first systematic investigation of physical contact and its role in social interactions between beluga mother–calf pairs, this study significantly contributes to our understanding of the use of contact during a critical period of development. Studying the first 2 y of life encompasses both the period of bond formation and solidification between mothers and their offspring prior to weaning as well as the development of calf–calf social interactions (Hill et al., 2013; Hill & Campbell, 2014; Krasnova et al., 2014). Several questions guided this initial examination of beluga calf tactile development:

1. What percent of *mother–calf* and *calf–calf* social interactions are spent in physical contact with one another?
2. Are there qualitative differences in the types (rub vs touch) of and body part(s) used for physical contact between mothers and calves during caregiving interactions, during affiliative social interactions, or during calf social interactions with others?
3. Who initiates physical contact during *mother–calf* interactions, whether caregiving or affiliative in nature?
4. Does the presence of contact influence the length of a social interaction?

Methods

Subjects and Facility

Five mother–calf beluga pairs housed at SeaWorld San Antonio served as study subjects. The calves were born between 2007 and 2010, and were housed within a relatively stable population that included one adult male and between one and three adult females without calves, depending on the year (for descriptive information, see Table 1). The beluga population inhabited a series of seven interconnected pools with the largest pool holding approximately 2 million gallons of water and was 31.8 × 15.2 m with an average depth of 7.6 m. Due to the staggered birth years and beluga relocations between facilities, the mother–calf pairs tended to be housed with each other. At times, one to two of the adult females were also included. During the first 2 y of life, none of the calves in this study were grouped with the adult male.

Different social compositions occurred throughout and across days. At most, four calves and their mothers were grouped together with access to at least two of the seven pools during this study. However, all calves had visual access to one another, with limited physical contact access when mother–calf pairs were separated into different pools that were connected with net walls and gates. Typically, mother–calf pairs were divided into two sets of pairs or three sets of pairs (e.g., the two male calves, OLI/GRA; the 2008/2009 female calves, QIN/BEL; the male calves and the 2008 female calf; and the 2008/2009/2010 female calves and male calf). These configurations ensured that calves always had access to at least one other calf and, more often than not, two or more after 2008. The fifth calf, ATL, did not bond with her mother but appeared to develop normally following a delay. She was included in this sample as she did engage in social interactions with other immature belugas.

Procedure

Video recordings were made from 2007 until 2012, using approximately 15 min of focal follow observations (range of selected videos: 6 to 15 min, $M = 13$ min, $SD = 3$ min) for each mother–calf pair. These video recordings represent data that are unique and entirely independent from the original studies conducted with this population of belugas during their first year of life with real-time ethogram data (Hill, 2009; Hill et al., 2013). Thus, the data from the current study are new and should not be considered a pseudo-replication of the previously published studies. Recordings (i.e., observations) were typically made one time a day per mother–calf pair, three to five times a week between 0700 and 1700 h. A delay of 10 to 15 min was instituted if more than one pair was recorded in the same day to ensure independence of observations between focal follows. The video recordings were collected using one of three available observation angles: (1) underwater through the glass pool wall, (2) above water from the side of the pool, and (3) above water from an elevated deck approximately 5 m above the pool surface. All video recordings were collected using the widest angle setting to record as much of the pool as possible while recording the mother–calf pair.

To equalize the amount of the available footage per mother–calf pair, four video recordings per calf per month were selected randomly with the rule that recordings collected from the underwater perspective would be prioritized for selection unless there were not enough in a given month and then one of the other recording perspectives would be randomly selected. Approximately 6% of the selected video recordings were collected from the underwater perspective. Video recordings were selected for each mother–calf pair from birth to 24 mo of life every other month. One calf was observed through 19 mo as his mother died at this time following a long-term illness.

Table 1. Demographic information for sample

Mother	Calf	Pair code	Sire	Year of birth	Sex	# calves available		Other adults (M:F)	
						Year 1	Year 2	Year 1	Year 2
TIN	OLI	TO	NAN	2007	M	1	2	1:4 ^a	1:3
MAR	GRA	MG	NAN	2007	M	1	2	1:4 ^a	1:3
SIK	QIN	SQ	NAN	2008	F	2	3	1:3	1:2
CRI	BEL	CB	A/I	2009	F	3	4	1:3	1:2
LUN	ATL	LA	NAN	2010	F	4	2	1:2	1 ^b :2

Note: A/I = artificial insemination. ^aThe two males were housed in a separate location from the beluga population from 3 wks to 10 mo at which time they were reintegrated with the rest of the population (see Hill, 2009, for specific details). ^bA new adult male was introduced into the population in 2011, replacing the adult male present between 2007 and 2010. The adult female composition and the calf composition changed in 2009 with new adult females added and previous adult females and two calves relocated to other facilities.

For each video recording, the focal animal was coded for duration of time the animal was visible to the coder (visible time), duration of time animal was not visible to the coder (non-visible time), and duration of each social interaction in which the focal animal was involved (i.e., event-sampling). Based on degree of visibility, social interactions were coded as either contact discernible or contact not discernible. For social interactions in which contact was discernible, coders recorded the duration of each contact event, the initiator, the receiver, and the body part used or contacted (see Table 2 for definitions). These coding rules represent the most conservative measure of contact and time spent in specific types of social activities.

Statistical Analyses

Each contact event was coded as a unique data point with an initiator, receiver, type of contact (touch/rub), interaction context, and duration. Although calves had varying amounts of time to

directly access each other, and this exposure may have affected the time calves spent with other calves, the conversion of each event to a rate using the amount of time within each social interaction in which an event occurred controlled for any difference in exposure time between individual pairs

To analyze the role of contact within the *context* of social interactions, contact events were aggregated for each social interaction into two key metrics: (1) percent of time spent in contact (sum duration of contact events by animal/duration of interaction) and (2) the rate of contact events (frequency of contact events/duration of interaction). Percent of time and rate capture different aspects of contact behavior, while both control for varying interaction durations. Percent of time captures contact events that occur infrequently but are longer in duration (e.g., infant swim position possibly or pectoral fin contact swimming), while rate of contact behavior captures contact events that occur frequently but are short in duration

Table 2. Operational definitions of activity bouts and contact events

Behavioral codes	Description
<i>Solo Activity Bouts</i>	A behavioral bout lasting more than 3 s that is not synchronous with, in close proximity to, or eliciting a response from other belugas
Solo swimming	Single beluga swimming at various speeds and directions
Solo playing	Single beluga engaged in object or motor play
Solo floating	Single beluga at the surface of the water but not moving through the water
<i>Social Activity Bouts</i>	When two or more belugas shift their behavior to share proximity (i.e., within one to two adult body lengths), involving an initiation or elicited response that involves some degree of synchrony or coordination
Affiliative interaction	Interaction with shared proximity that is non-aggressive and non-sexual in nature
Sexual interaction	Interaction which involves the contact with or the presentation of the genitals or genital region
Aggressive interaction	Interaction that is performed with force and produced to threaten or displace another beluga (e.g., chases that involve bite attempts, biting, or raking)
Echelon swim	Interaction in which calf is positioned just above and slightly to the side of the mother's or other beluga's dorsal ridge
Infant swim	Interaction in which calf is positioned just under the mother or other beluga with head located near the mammary slits (Figure 1)
Pair swim	Interaction in which the calf is positioned above, below, or to the side of the mother or other beluga, excluding echelon and infant positions
<i>Contact Events</i>	A discrete occurrence of physical contact between two belugas, separated from other contact events by either a lack of contact or a shift in the type of contact (e.g., body part used or a shift from static to dynamic; see Figure 2)
Rub	A dynamic tactile stimulation that starts at one point and ends at a different point on the recipient's body; may be initiated with a pectoral fin, a portion of the body or the full body, a head, or flukes.
Touch	A static contact point that does not change from its initial contact point, ending when the contact point is terminated; may be initiated with a pectoral fin, a portion of the body or the full body, a head, or flukes.



Figure 1. Mother-calf dorsal-to-ventral contact as calf moves from infant position (*Photo credit:* Heather Hill)



Figure 2. Picture of fluke-to-body social contact initiated by a calf toward his mother (referred to in Table 1) (*Photo credit:* Heather Hill)

(e.g., bumping in calves or goosing of genitalia). Both measures are necessary to interpret the possible functions of contact in social interactions. All measurements referencing contact (e.g., rates or durations of contact) are calculated from the total social observation time when contact was discernible (20.82 h).

Data were collapsed across the 2 y of life to examine overall trends using total frequencies and averaged percentages and rates for each pair when appropriate. Chi square goodness of fit tests were conducted to examine the frequencies of preferences for types of interactions and body parts used. Between subjects 3-way ANOVAs and independent *t* tests were performed when data from all individual events were used to examine the duration of each behavioral category of interest and the percent of contact during different types of interactions. Year and behavioral category were considered fixed factors, while mother–calf pair was considered a random factor (Field, 2009). Sidak *post hoc* tests were performed to investigate significant main effects.

Results

Descriptive Statistics for Time in Coded Activities General Activities—Out of 230 video recordings from five mother–calf pairs, 50.01 h of observation were collected. About 6.5% of this footage was excluded because an animal was not visible (2.19 h) or time engaged in activity was not coded in this study (1.09 h). Ultimately, a total of 46.22 h of social interactions and solitary activities was coded: 56% contained social interactions between animals, and 44% consisted of solitary activities (Table 3). About 80% of the coded footage was spent in social activities (25.88 h) with visibility necessary to discern contact (20.82 h).

Social Interactions—Collapsed across the first 2 y of life for all subjects, mothers and their calves swam within two adult body lengths of one another in a synchronized or coordinated manner or were within proximity of one another engaging in an affiliative social interaction 48% of the total visible coded activity time (Table 3). Calves spent 5.0% (2.31 h) of coded visible

Table 3. Descriptive statistics for main categories of activity bouts and contact

	Total (h)	Average duration $M \pm SD$ (s)	Contact discernible hours (%)	Sum contact (h)	Average contact % $M \pm SD$	Average rate of contact (min)	Contact duration $M \pm SD$ (s)	Touch %/ Rub %
Videotaped observation time	50.01							
Visible coded activity time	46.22							
Total calf solitary activities	20.34	47.8 \pm 86.8						
Total mother–calf time	22.38	76.0 \pm 116.8	18.41 (83.3%)	5.64	26.0% \pm 52.6	1.6 \pm 3.4	24 \pm 63	64/36
Infant position	8.02	113.2 \pm 133.8	7.58 (94.5%)	4.98	74.5% \pm 77.7	2.3 \pm 3.8	83 \pm 100	92/8
Echelon	2.55	63.9 \pm 103.9	2.20 (86.2%)	0.24	14.7% \pm 30.8	1.7 \pm 3.4	7 \pm 26	37/63
Pair	6.30	77.5 \pm 122.8	5.18 (82.2%)	0.21	6.1% \pm 17.6	0.9 \pm 2.4	3 \pm 15	48/52
Affiliative	5.51	53.9 \pm 96.2	3.45 (62.6%)	0.20	8.7% \pm 20.0	1.7 \pm 3.8	3 \pm 7	32/68
Calf–calf time	2.31	31.1 \pm 36.2	1.47 (63.7%)	0.13	9.3% \pm 19.3	1.9 \pm 5.3	3 \pm 7	51/49

Note: Visible coded activity is the sum of all time when the coder indicated an activity bout and a duration. Includes the categories reported in the table as well as 1.2 h of time in various other types of interactions. Total hours is the sum of time spent in the activity. Average duration was calculated by duration of each activity bout divided by the total frequency of the activity. Contact discernible hours is the time in that interaction in which the coder indicated that contact was discernible. Average contact % was calculated by the percent of contact for each duration activity bout observed divided by the frequency of the activity to illustrate the average amount of contact for each activity bout. Touch and rub percentages were calculated by the frequency of that type of contact out of the total contact in the interaction type. Average rate of contact is calculated from the events per minute of activity bout when contact was discernible.

activity time (46.22 h) engaged in affiliative interactions with other calves. Solitary activities accounted for 44% (20.34 h) of their time. The remaining time (1.19 h, 2.6%) included a variety of social interactions that did not involve other calves or their mothers. Group interactions involving other mother–calf pairs (0.40 h, 0.9% of total interaction time), affiliative interactions with adults who were not their mothers (0.38 h, 0.8%), or aggressive interactions between calves and adults (0.05 h, 0.1%) accounted for the majority of this time. One social interaction, a short agonistic encounter, was observed between two adult females; and several short, social interspecies interactions occurred with the dolphins housed in the same area. Finally, of the time mothers and calves spent together (22.38 h), infant swimming occurred 35.8% (8.02 h) of the time, other forms of pair swimming totaled 28.2% (side-by-side: 16.8% [2.55 h]; echelon: 11.4% [6.30 h]) of the time, and affiliative interactions with each other occurred 24.6% (5.51 h) of the time (Table 3).

Physical Contact

Beluga calves did not engage in physical contact with another individual for 71% of the total social interaction time when contact was discernible. A total of 5.98 h of contact were measured across 2 y of life for four of five beluga mother–calf pairs combined as the fifth calf (ATL) did not bond with her biological mother (LUN) and was hand raised by trainers but socially housed with LUN. The majority of contact (94%, 5.64 h) occurred between mother–calf pairs, while contact between calves only accounted for 2% (0.13 h) of the total duration of contact time measured. The remaining time of contact (3.5% or 0.21 h) accounted for all interactions outside of the primary mother–calf and calf–calf categories. Only one instance of contact was observed between two adult females.

Time Spent in Contact—Mother–calf infant swims had the greatest amount of contact across social interactions. On average, 74.5% of the duration of mother–calf infant swims was spent in contact, with each contact event lasting an average of 83 s (Table 3). The second highest contact interaction type was mother–calf echelon

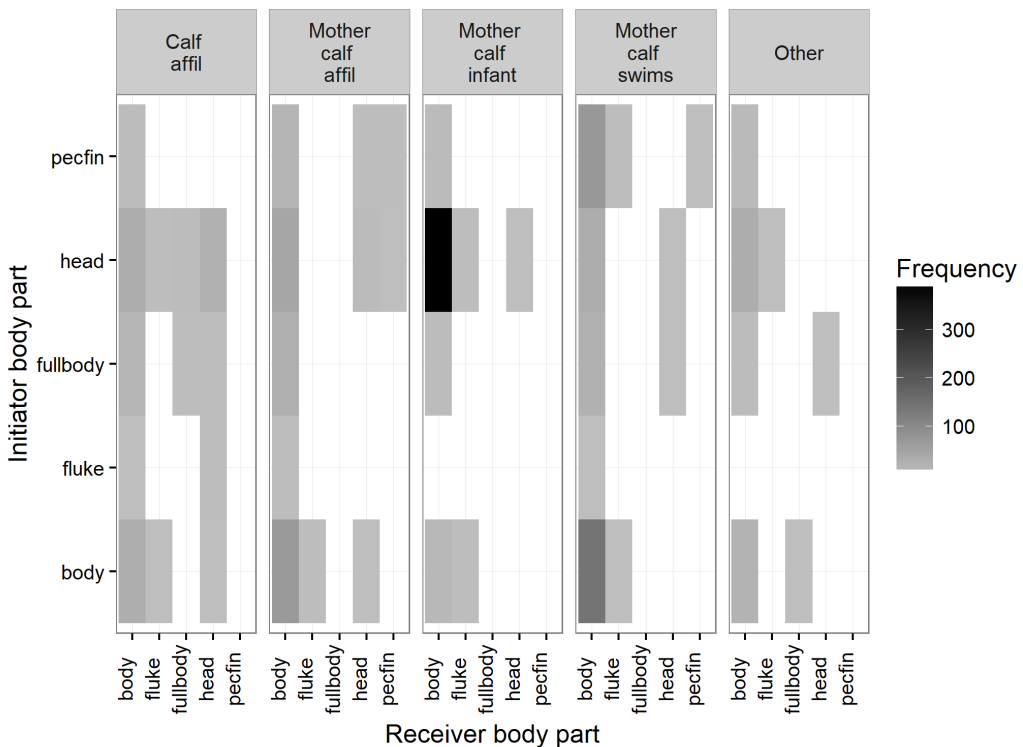


Figure 3. Cross-tabulation of initiator body part, receiver body part, and the type of social interaction in which contact occurred

swims (14.7%, ~ 7.3 s) (Table 3). Mother–calf and calf–calf affiliative interactions had similar levels of contact: 8.7% (SEM = 0.9%, $n = 609$) of mother–calf and 9.3% (SEM = 1.5%, $n = 176$) of calf–calf affiliative interactions were spent in contact (independent t test, $p > 0.05$). Contact durations for mother–calf ($M = 2.8$ s) and calf–calf ($M = 2.7$ s) affiliative interactions were also similar (independent t test, $p > 0.05$) (Table 3).

Frequency of Contact—When frequency of physical contact was examined, contact between mothers and calves occurred at a rate of 1.6 events/min of social interaction. Mother–calf infant swims had the highest rate of contact, followed by contact during mother–calf echelon swim and contact during mother–calf affiliative interactions. The rate of contact during mother–calf side-by-side pair swims was almost half the rate of other forms of mother–calf social interactions (Table 3). Contact between calves during affiliative interactions occurred at similar rates as contact during mother–calf affiliative social interactions (Table 3).

Characteristics of Contact During Social Interactions

Caregiving-Based Social Interactions—Of the infant position contact events ($N = 420$), 92% ($n = 388$) were static, sustained touches with the infant head to the mother's body. Of contact in echelon position ($N = 139$), 75% ($n = 104$) were body-to-body (including portion of the body and full-body contact) (63% rubs, $n = 87$; 37% touches, $n = 52$), while 20% were pectoral-fin-to-body (64% rubs, $n = 18$; 36% touches, $n = 10$). During mother–calf side-by-side pair swims ($N = 145$), body-to-body contact was the most frequent type of contact (45.5%, $n = 66$), followed by pectoral-fin-to-body contact (31.0%, $n = 45$) and head-to-body contact (18.6%, $n = 27$). Of these contact events during mother–calf side-by-side pair swims, 54.4% were rubs ($n = 76$). These patterns are summarized in Figure 3.

Affiliative Social Interactions—During affiliative interactions between mother–calf pairs, body-to-body (including portions of the body and full-body contact) was the most frequently occurring contact event (54.45%, $n = 97$), followed by head-to-body (25.8%, $n = 46$) (test of independence $\chi^2(9, N = 178) = 21.53, p = 0.01, V = 0.20$) (Figure 3). The largest number of rubs observed between calves and their mothers occurred during affiliative interactions ($n = 121$), which deviated significantly more than expected by chance (goodness of fit $\chi^2(3, N = 316) = 51.22, p < 0.001$) (Figure 3). During affiliative interactions with other calves, body-to-body contact again occurred significantly more often

(38.4%, $n = 48$), followed by head-to-body contact (29.6%, $n = 37$) and head-to-head contact (20.8%, $n = 26$) as compared to any other category (goodness of fit $\chi^2(6, N = 125) = 23.60, p = 0.001$) (Figure 3). Calves were equally likely to contact each other during affiliative interactions with rubs ($n = 61$) or touches ($n = 64$).

Pectoral Fin Contact—When comparing pectoral fin contact across all mother–calf social interactions ($n = 97$), 46.4% ($n = 45$) pectoral-fin-to-body contact events were observed during mother–calf side-by-side pair swims, 20% ($n = 28$) pectoral-fin-to-body contact events during mother–calf echelon swims, 10% ($n = 17$) pectoral-fin-to-body contact events during mother–calf affiliative interactions, and 2% ($n = 7$) pectoral-fin-to-body contact events during mother–calf infant swims. Only one pectoral-fin-to-body contact was observed during a calf–calf affiliative interaction.

Initiators of Social Interactions and Physical Contact

Collapsed across both years, mothers initiated 55.5% ($n = 584$) of the social bouts with their calves, and calves initiated 44.5% ($n = 469$) of the social bouts with their mothers (binomial test, $z(N = 1,053) = -3.51, p < 0.001$). Calves, however, initiated the majority of *physical contact* events with their mothers (98%, $n = 863$) (binomial test, $z(N = 904) = 28.57, p < 0.001$). Mothers initiated 2% ($n = 19$) of contact events with their calves and did not initiate any contact with other calves.

Duration of Social Interactions and Physical Contact Events

Duration of Select Social Interactions—Although mother–calf swims (echelon and side-by-side swims) lasted longest on average, they were not significantly different in average duration from mother–calf affiliative interactions or from calf–calf affiliative interactions (Table 3) per the results of a 5 (mother–calf pair) \times 2 (year) \times 3 (social interaction) ANOVA using all individual events identified per category.

Duration of Social Interaction Based on Physical Contact—Three independent t tests were conducted to determine if the average duration of a behavioral context differed based on the presence or absence of physical contact. The results indicated that the average duration for each behavioral category tested (i.e., calf–calf affiliative interactions, mother–calf affiliative interactions, and mother–calf swims, excluding infant position) was significantly longer when contact was present during the interaction than when contact was absent (Table 4).

Table 4. Descriptive and inferential statistics for average length (s) of social interaction as influenced by contact

	Contact present			Contact absent			<i>t</i>	df	<i>p</i>
	<i>M</i>	SE	<i>n</i>	<i>M</i>	SE	<i>n</i>			
Calf–calf affiliative	43.58	5.12	66	26.97	3.34	202	2.95	93.70	0.004
Mother–calf affiliative	76.47	13.99	96	45.90	4.58	272	2.08	116.02	0.040
Mother–calf swims	113.23	12.72	130	55.93	5.60	307	4.12	181.03	< 0.001

Note: Calf–calf affiliative included positive types of social interactions, including pair swims that calves exhibited with other calves. Mother–calf affiliative included any types of positive social interactions that were not related directly to the survival of the calf. Mother–calf swims included echelon and side-by-side pair swims. Infant position was excluded for this analysis.

Discussion

Using a unique set of longitudinal data, the current study systematically addressed the nature of tactile contact during social interactions displayed by five beluga calves during their first 2 y of life. Because of their staggered births, all calves had at least one and up to four peers of similar age throughout their first 2 y of life. We first describe the types of social interactions observed during this time frame, and then discuss the characteristics and possible functions of contact experienced by these calves.

Time Swimming or Socializing with Other Belugas

Four of the observed study calves spent most of their time swimming in infant position with their mothers followed by side-by-side pair swims and echelon swims, much like free-ranging beluga calves and delphinids in both managed care and their natural habitat (Gubbins et al., 1999; Mann & Smuts, 1999; Weihs, 2004; Krasnova et al., 2006, 2009, 2014; Noren et al., 2006, 2008; Lyamin et al., 2008; Noren & Edwards, 2011). Affiliative forms of social interactions with their mothers, such as play bouts and nuzzling, occurred about as often as side-by-side pair swims, both of which have been observed, but not quantified, in free-ranging beluga mother–calf pairs (Krasnova et al., 2006, 2009, 2014). Like delphinid calves (Mann & Smuts, 1999; Mackey et al., 2014; Guarino et al., 2016), social interactions, such as play bouts, chases, and pair swims between calves, accounted for about 5% of the visible time. The fifth calf did not bond with her mother and was observed mostly engaged in solitary activities when she was not interacting with other similar-aged peers.

Physical Contact During Social Interactions

Like many other species, the majority of social interactions between beluga calves and their mothers or other calves occurred without physical

contact. As expected from previous observations of delphinids (Mann & Smuts, 1999; Miles & Herzing, 2003) and belugas (Krasnova et al., 2006), most observed physical contact occurred between calves and their mothers, with calves initiating almost all recorded contact events; this had not been systematically examined in earlier research. As expected from time spent together swimming in infant position, the greatest proportion of mother–calf contact occurred during this swim position. This position is observed universally across all cetaceans studied thus far, likely because it significantly contributes to the survival of the calf for reasons discussed earlier, including proximity to mother for safety, rest, nutrition, learning opportunities, and bonding (Herman & Tavolga, 1980; Gubbins et al., 1999; Mann & Smuts, 1999; Weihs, 2004; Krasnova et al., 2006; Noren et al., 2006, 2008; Lyamin et al., 2008; Noren & Edwards, 2011).

In delphinids, echelon position does not occur as often as infant position and tends to decrease as a calf ages through the first year of life, likely in part because the benefits from slip-streaming and camouflaging are lost as the calf grows and becomes a more efficient swimmer (Gubbins et al., 1999; Weihs, 2004; Noren et al., 2006, 2008; Lyamin et al., 2008; Noren & Edwards, 2011). A similar pattern was observed for these belugas with echelon swims occurring, but less often than infant or side-by-side pair swims. Calves spent more time engaged in contact during echelon than in side-by-side swims despite spending more time swimming next to their mothers. This pattern is likely because echelon swimming was observed when calves were younger, with less motor control and with inefficient respirations (Mann & Smuts, 1999; Weihs, 2004; Lyamin et al., 2008; Noren et al., 2008)

Of particular interest was the time calves spent engaged in physical contact with their mothers during affiliative social interactions. As these social interactions do not directly meet any

immediate calf survival needs, it is probable that contact during these affiliative interactions functions to strengthen the bond formed between the calves and their mothers, which ultimately would increase calf survival. This conclusion is also likely for contact exchanged between calves.

The amount of time calves socialized with their mothers was more than twice that of other calves; however, when quantity of physical time during affiliative social interactions was compared directly, both the proportion of time and duration of contact time were similar between mother–calf pairs and calf–calf pairs. Moreover, the same body part (i.e., body-to-body and head-to-body) was used preferentially by calves when initiating contact with their mother or another calf. Calves rubbed their mothers significantly more during affiliative social interactions whereas they used both touches and rubs with other calves. The nature of contact during affiliative social interactions is qualitatively and quantitatively different from contact performed by calves when engaged in social interactions that directly affect their survival. Ultimately, all forms of social interactions with contact exchanges documented among belugas in this study lasted significantly longer than social interactions without contact.

Pectoral Fin Contact—Although not observed frequently like dolphins (Dudzinski, 1998; Sakai et al., 2006; Tamaki et al., 2006; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017), beluga calves used their pectoral fins to make contact with their mothers during mother–calf affiliative social interactions. It seemed that calves preferred to use their heads and bodies when initiating contact with each other. Only four pectoral fin contacts were observed between calves during this study, much like juvenile Atlantic spotted dolphins (*Stenella frontalis*) (Kaplan & Connor, 2007). We encourage future research to examine pectoral fin contact exchanges more closely in belugas with calves that are older than a year. Although it is possible that our calves were too young to display pectoral fin contact, it is more likely that our sampling method and external video recordings may not have had the same opportunity to capture pectoral fin contacts as the underwater recording technique used by Dudzinski in her research (Dudzinski, 1998; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017). More research is needed to clarify if pectoral fin contact is a significant factor in the development or maintenance of social bonds for belugas as it seems to be for delphinids (Dudzinski, 1998; Sakai et al., 2006; Tamaki et al., 2006; Kaplan & Connor, 2007; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017).

Does Contact Play a Significant Role in Beluga Calf Social Interactions?

Our observations suggest that contact plays a significant role in beluga calf social interactions using two pieces of evidence: (1) longer social interactions occurred when contact was present than when it was absent during interactions with their mothers and with other calves, and (2) calves engaged in contact equally during affiliative interactions with either their mothers or other calves. In contrast, contact does not seem to be a significant aspect of social interactions between adult females or between females and non-biological calves in this population. In fact, social interactions in general did not occur often between these animals. It is currently unclear if the lack of social interactions between adult female belugas or between mothers and unrelated calves were specific to this population, related to the social groupings in which they were housed, or a valid finding that should be examined further with other populations in both managed care and their natural habitat.

Belugas are described as highly gregarious due to their tendency to be found in large congregations (Bel'kovitch & Sh'ekotov, 1993; O'Corry-Crowe et al., 1997; Colbeck et al., 2013; Krasnova et al., 2014), and anecdotal reports suggest that when free-ranging belugas inhabit shallow estuaries, adults physically contact one another frequently during social activities, including socio-sexual interactions (Michaud, 2005; Krasnova et al., 2014). Yet, a systematic investigation of physical contact conducted with the full beluga population from the same facility at a separate time from the current study indicated that contact occurred most frequently between a mother and her 3-y-old calf, immature belugas, and male belugas of different age classes (Hill et al., 2016). Almost no contact occurred between unrelated adult females or between adult females and males outside of the breeding season (Hill et al., 2016). These patterns of contact have been corroborated by anecdotal observations of unrelated adults from other beluga populations in managed care as reported informally by trainers and researchers (Glabicky et al., 2010; but see Recchia, 1994, for a possible exception).

The reports on free-ranging belugas represent qualitative assessments based on general observations of animals whose identity may be ascertained reliably but for which relatedness may not be clear (Michaud, 2005; Krasnova et al., 2006, 2014). In the current study, relatedness is known and, importantly, with each additional calf, the number of available adult females without calves decreased, which reduced the availability of potential allomaternal caregivers and possibly impacted the frequency of contact between calves and other adult females (Hill & Campbell, 2014; Krasnova et al., 2014).

We propose three possible explanations for these differences in observed contact between the systematic study involving belugas in managed care (i.e., the current study; Hill et al., 2016) and anecdotal observations of free-ranging belugas (Michaud, 2005; Krasnova et al., 2014). First, belugas are able to swim in close proximity without contacting one another, much like delphinids (e.g., Mann & Smuts, 1999). Even with the controlled water quality of the current study, glare from sunlight or limited visibility in shaded areas made it difficult to observe contact occurring under water. With more turbid waters in the natural habitat, it is possible that one could observe wild belugas swimming in close proximity and infer physical contact when it is not present. Currently not empirically tested, it is likely that animals swimming in close proximity sense the location of their partner through the displacement of water or when eavesdropping on their partner's echolocation while swimming (e.g., Xitco & Roitblat, 1996; Gregg et al., 2007). The present study focused exclusively on tactile contact and excluded other ways to sense closeness. Future research should examine these different aspects of contact.

Second, it is possible that contact observed between adult belugas in the wild is disproportionately represented by contact between males. Physical contact may be an important component for adult male belugas and juvenile belugas as brief, physical contact events have been observed frequently during socio-sexual bouts between adult males and/or juveniles of both sexes in managed care (Glabicky et al., 2010; Hill et al., 2015; Miller & Hill, 2015). Given that adult females in managed care do not appear to engage in the same types of socio-sexual behaviors, contact between male adults and/or male and female juveniles may be significant in the bonding process (Glabicky et al., 2010; Hill et al., 2015; Miller & Hill, 2015). Research with juvenile Atlantic spotted dolphins supports this possible explanation (Kaplan & Connor, 2007). Male belugas in their natural habitat spend much of their time traveling together (Colbeck et al., 2013), similar to the more frequently studied dolphin species in which adult male dolphins spend more time together than adult female dolphins (Elliser & Herzing, 2014; Connor & Krützen, 2015; Smith et al., 2016).

Finally, the female adult belugas in the present study were not directly related and were not raised together. Female calves observed in the study continued to contact their mothers and other belugas in their cohort even as they matured through the second year. It is possible that social bonds facilitated through contact are developed at young ages and sustained throughout the lifespan. Only systematic studies of contact with known individuals of confirmed sex, age, and relatedness

across various populations will be able to definitively distinguish the role of contact in beluga social interactions across the lifespan. These studies have begun to be conducted with dolphins in both natural habitats and managed care, and they currently indicate that there are no differences in contact patterns when free-ranging and captive animals are directly compared (Dudzinski et al., 2009, 2010, 2012).

Ultimately, physical contact appears to be used differently depending on the social interaction and participants. First, the context in which physical contact occurred was related to the body part used during the contact event. Calves preferred to use their bodies (as opposed to their head, pectoral fins, or flukes) to initiate contact with their mothers during different swim positions and affiliative social interactions. Second, the type of contact, a static touch or a dynamic rub, varied between types of social interactions and partner classes. Calves tended to rub their mothers during mother-calf interactions and touch each other during calf-calf social interactions. In particular, calves rubbed their mothers during mother-calf swims not involving infant position and during affiliative interactions, but they touched other calves during affiliative social interactions. These results may be related to the duration of the different social interactions (i.e., mother-calf swims were longer on average than mother-calf affiliative interactions and calf-calf affiliative interactions but not statistically different) such that longer duration interactions can provide more opportunities for rubs. However, rubs may also represent a more dynamic and prolonged means to facilitate bonding, and additional research is necessary to determine their role in contact. Continuous underwater footage would elucidate these results by providing a more accurate representation of contact that is not as easy to obtain from surface-based recordings. The present study incorporated data collected from both perspectives, which may account for the degree of variability observed in duration.

More directed research on physical contact across multiple beluga populations is also needed to clarify the importance of contact in the development of the mother-calf bond and other calf associations. First, underwater footage of the first few months of life should be examined to determine if a physical-based bond begins immediately upon birth (e.g., imprinting) or if it takes time to develop (e.g., attachment). Second, more studies need to be conducted beyond the first year of life, especially for cetaceans in controlled environments. The majority of the developmental studies on cetaceans end sometime during the first year of life or only use limited samples (e.g., Reid et al., 1995; Gubbins et al., 1999; Hill et al., 2007, 2013;

Hill, 2009). Topics such as the process or consequences of weaning, the characteristics of the juvenile period, the influence of early associations on future behavior, and reproductive success have begun to be addressed in cetacean populations with long-term field studies (e.g., Sarasota, Shark Bay, and Bahama dolphins). Similar types of studies in controlled environments are emerging and should be continued as these studies provide some of the best visibility and opportunities to observe many of the phenomena mentioned above (Samuels & Tyack, 2000; Perelberg et al., 2010).

Conclusion

The results of this 2-y longitudinal study suggest that tactile contact is particularly important to the social interactions of beluga calves with their mothers and other calves. Moreover, the frequency with which calves contact other calves, including calves of different ages, suggests that belugas may use contact to establish bonds with each other at young ages. However, the development of calf-calf bonds may depend on the sex and age of the belugas involved. Like many other aquatic and terrestrial animals (e.g., Pereira & Fairbanks, 1993; Dudzinski, 1998; Lee & Moss, 1999; Kaplan & Connor, 2007; Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017), recent research on the socio-sexual behavior of belugas suggests that sex differences may exist for social interactions in which juvenile, sexually maturing, and sexually mature males engage in more social interactions and bonding than sexually mature females, while immature females fall somewhere between these groups (Glabicky et al., 2010; Hill et al., 2015). Future research should examine whether this early bonding is maintained once the calves reach sexual maturity; and if it is, does contact continue to play a role in those bonds or does it change based on the sex of the beluga?

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