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The Frequency and Nature of Allocare by a Group of Belugas (*Delphinapterus leucas*) in Human Care

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The care of offspring by non-parental caregivers, or allocare, is common across many taxa. Several functions of allocare have been proposed, including opportunities to rest or forage for the mother, experiences to learn about caring for young animals for naïve females, or additional nourishment and protection for the offspring. Belugas, like many cetaceans, display allocare. However, the frequency and contexts in which allocare occurs have not been studied extensively. The purpose of the current study was to document the frequency of allocare in a group of belugas in human care that steadily increased in its number of offspring over a period of four years. The results suggested that allocare did not occur as frequently as mother-calf swims and occurred when adult females without calves were available in the social grouping. Additionally, certain allocare partners seemed to be preferred by specific mother-calf pairs. The results also indicated that the calf may play a more active role in the selection of an allocare partner than previously acknowledged. This study supports the importance of social composition when young offspring are present.

Allocare, allomaternal care, allopaternal care, alloparental care, or babysitting, are the range of terms that describe various contexts in which older juvenile or adult conspecifics other than a primary caregiver cares for a young animal when the caregiver is unavailable (Gero, Engelhaupt, Rendell, & Whitehead, 2009; Howells et al., 2009; Leung, Vergara, & Barrett-Lennard, 2010; Mann & Smuts, 1998; Packer, Lewis, & Pusey, 1992; Riedman, 1982; Schubert, Pillay, & Schradin, 2009; Whitehead, 1996). Allocare events deviate from typical social interactions as allocare providers must alter their behavior to care for the young animal in the absence of the primary caregiver. Thus, allocare providers experience a cost in various resources while the young animal and its primary caregiver benefit from the epimeletic behavior (Leung et al., 2010; Packer et al., 1992; Riedman, 1982; Roulin, 2002; Whitehead, 1995, 1996; Whitehead & Mann, 2000, Woodroffe & Vincent, 1994).

In 1982, Riedman wrote a comprehensive review of the current understanding of allomaternal care in mammals and birds. She not only summarized the various animals in which allomaternal care had been documented (e.g., eusocial insects, fish, birds, terrestrial and aquatic mammals), she also discussed a variety of variables that appeared to influence the presence of allocare. As described by Riedman, "social organization, behavioral ecology, certain life-history and reproductive parameters, and degree of kinship between individuals" (p. 427) are all variables that determine allocare and have been supported by more

recent research. For example, a quantitative analysis of various parameters collected for 44 species indicated allocare was more likely to occur in cooperative breeders that live in smaller social groupings with high levels of relatedness (Briga, Pen, & Wright, 2012). This analysis also verified that allocare was exhibited by species without cooperative breeding, living in groups with few related individuals and high levels of offspring care (Briga et al., 2012).

The degree of investment by the non-parental care provider varies across species and individuals as well (Lewis & Pusey, 1997; Komdeur, 2006; Riedman, 1982; Trivers, 1971). A direct investment of a non-mother care provider requires a higher degree of resources when interacting with a young conspecific. Examples of direct investment behaviors include grooming, maintaining contact or proximity, carrying, provisioning with food, nursing, or protecting the young conspecific physically from threats. An extreme case of direct investment is the adoption of another animal's offspring (Riedman, 1982). Comparatively, indirect investment depends on fewer resources as the non-mother care provider does not interact with the young conspecific. Instead, the non-mother care provider may increase vigilance while young are present, engage in territorial defense, or display herding movements.

In species with uniparental care of precocial young living in exposed habitats (e.g., elephants, ungulates, and marine mammals), allocare occurs and is associated with the increased survival of the young (Bates et al., 2008; Gero et al., 2009; Reidman, 1982; Stanton & Mann, 2012; Wells, 2003; White & Cameron, 2011; Whitehead, 1996). Marine mammals, like cetaceans, are generally described as polygamous with mothers performing all offspring care during the dependent period (for an exception see Byerly, Richardson, & Kuczaj, 2009). In their natural habitat, many cetaceans form nursery groups during the early stages of the dependence period but will interact with other female conspecifics as calves mature (belugas: Krasnova, Bel'kovich, & Chernetsky, 2006, 2009; for a general review see Whitehead & Mann, 2000). These larger social groups provide opportunities for allocare as females without their own offspring are more likely to provide care for a conspecific's offspring (Riedman, 1982).

Like other group-living mammals, cetaceans exhibit allocare behaviors that range in degree of investment, from a minimal cost of remaining vigilant when part of a social group with calves to a maximum cost of providing nutrition through lactation or physical protection of a calf during a direct threat to the calf (belugas, *Delphinapterus leucas*: Bel'kovitch & Sh'ekotov, 1993; Leung et al., 2010; bottlenose dolphins, *Tursiops* spp.: reviewed by Whitehead & Mann, 2000; Gaspar, Lenzi, Reddy, & Sweeney, 2000; killer whales, *Orcinus orca*: Waite, 1988 as cited in Leung et al., 2010; sperm whales, *Physeter macrocephalus*: Gero, Engelhaupt, Rendell, & Whitehead, 2008, 2009; Whitehead, 1996). One set of long-term studies on sperm whales suggested that two possible mechanisms may have driven the presence of allocare in different sperm whale groups (Gero et al., 2008, 2009): kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971). Using data collected from two distinct geographical sperm whale populations, Gero and his colleagues (2009) concluded that in highly stable and small social groupings, individuals that were genetically related to the calf were more likely to care for the calf when the mother was away, kin selection. In contrast, sperm whale mothers living in larger social groupings with their calves were more likely to engage in allocare events with mothers that had calves of similar ages, reciprocal altruism. Similarly, free-ranging bottlenose dolphins may support a third mechanism for allocare: "learning to mother," in which younger, less experienced female adults and sub-adults care for neonates or young offspring (Mann & Smuts, 1998). Of the allocare studies that have been conducted with cetaceans in human care (see review by Whitehead & Mann, 2000; Leung et al., 2010; Winhall, 2012), most of these have focused on nursing behaviors, including spontaneous lactation.

The purpose of the current study was to document the frequency and context of allocare behaviors in a group of breeding white whales (belugas) in human care. A highly reactive species to environmental threats, belugas are native to Arctic to sub-Arctic waters surrounding Alaska, Canada, and Russia. They

travel into the estuaries during the summer months for feeding and calving, creating nursery groups typically within their natal range (Bel'kovitch & Sh'ekotov, 1993; Brown Gladden, Ferguson, & Clayton, 1997; O'Corry-Crowe, Suydam, Rosenberg, Frost, & Dizon, 1997; O'Corry-Crowe, 2009). Observations of nursery groups have suggested that free-ranging adolescents remain with calves (i.e., allocare) while the adult females forage, thereby potentially increasing the fitness of the calves (Bel'kovitch & Sh'ekotov, 1993; Krasnova et al., 2006, 2009). Case studies of belugas in human care, in which spontaneous lactation and care by unrelated females for calves were observed, support the possibility that allocare is part of the behavioral repertoire of belugas (Leung et al., 2010; Winhall, 2012).

Unfortunately, these studies do not clarify the extent to which allocare occurs in belugas either in their natural habitat or in controlled environments. Moreover, these studies on belugas, nor most studies with cetaceans, have explored fully the nature (e.g., frequency, duration, initiators) of allocare behaviors. The birth of five beluga calves over a four year period at a North American facility provided an opportunity to examine the frequency and nature of allocare in a controlled setting. Based on the previous literature, several questions guided our study:

(1) How often did allocare occur in this population of belugas?
(2) What was the nature of allocare events in these belugas?
(3) Which animal initiated the allocare event: the mother, the calf, or the allomother?
(4) How did allocare events compare to typical mother-calf interactions?

Method

Subjects and Facility

Five calves born at SeaWorld San Antonio (SWSA) between 2007 and 2010 were examined for the current study. Table 1 summarizes all relevant demographics and significant relationships of all belugas present at the facility across the four year period. The facility in which the belugas were housed contained seven interconnected pools. The largest pool was Pool A, or the birth pool, and was the only pool with underwater viewing. All other pools had only above water viewing (Figure 1). Once mother-calf bonds were established, all pairs were given access to different combinations of the seven pools based upon trainer-determined groupings. Four to eight additional belugas resided at the facility during the study period and remained relatively stable with regards to social composition. Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) also resided at this facility but were not housed in the same pool as belugas.
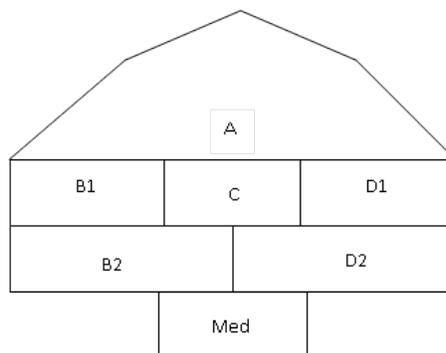
Figure 1. Schematic of pool layout of SeaWorld San Antonio facility. Pools are not drawn to scale. Gates connected all pools together. The triangular-shaped, A pool, held approximately 2 million gallons and was about 38.1 m (125 ft) by 15.2 m (50 ft) with an average depth of 7.6 m (about 25 ft). The secondary housing for the first two calves, the zoological pool, had the following approximate dimensions: 17.1 m (56 ft) x 10.7 m (35 ft) x 6.1 m (20 ft).

Two male calves (OLI, GRA) were born three days apart in June 2007 and shared the same sire (Table 1). Both calves were birthed and housed at the main facility for two weeks. Both mother-calf pairs (TIN-OLI, MAR-GRA) were transferred to a different pool within the zoological area of SWSA for veterinary care purposes. Both pairs remained at this location until 10 months of age when they were returned to the primary facility and integrated with the four other adult belugas, three adult females and one adult male.

Table 1. *Demographic information for belugas.*

Animal	Sex	Age Status	Birth Year	Parity	Relationships	Arrival at Facility
TIN	F	Adult	*	Multiparous	Mother: LUN, OLI	**
OLI	M	Calf	2007		Offspring: TIN	2007
					Brother: LUN, GRA	
MAR	F	Adult	*	Primiparous	Mother: GRA	**
GRA	M	Calf	2007		Offspring: MAR	2007
					Brother: OLI	
SIK	F	Adult	*	Primiparous	Mother: QIN	**
QIN	F	Calf	2008		Offspring: SIK	2008
CRI	F	Adult	*	Multiparous	Mother: WHI, BEL	**
BEL	F	Calf	2009		Sister: WHI	2009
LUN	F	Adult	2000	Primiparous	Mother: ATL	2000
					Offspring: TIN	
					Sister: OLI	
ATL	F	Calf	2010		Offspring: LUN	2010
					Niece: OLI	
WHI	F	Adult	1999	Primiparous	Offspring: CRI	1999
					Sister: BEL	
BET	M	Adult	1992			1992, 2007
NAT	F	Adult	*	Multiparous		2009
IMA	M	Adult	*			2011

Note. * indicates animal was born in natural habitat and entered human care during the 1980s. ** indicates animal resided at facility before current study initiated in 2007.

A female calf (QIN) was born July 2008 at SWSA (Table 1). This mother-calf pair (SIK-QIN) was integrated with the other belugas shortly after birth. These belugas included two adult females (WHI, LUN), the two mother-calf pairs from the previous year (TIN-OLI, MAR-GRA), and occasionally, an adult male (BET).

The second female (BEL) was born June 2009 at SWSA (Table 1). This pair (CRI-BEL) was initially integrated with the third calf (QIN) and her mother (SIK). Across the first year, the newest mother-calf pair was housed in various groupings, including the mother-calf two-year old males and their mothers, the one-year old female and her mother, and the two adult females present the previous years. Additionally, two new belugas (an adult female, NAT, and adult male, IMA) were added to the population while the adult male (BET) was transferred to another facility (Table 1).

Finally, the fifth calf (ATL) was a female born in June 2010 to one of the adult females (LUN) that acted as a companion to the four other mother-calf pairs (Table 1). This mother-calf pair (LUN-ATL) did not bond with each other. The pair was immediately integrated with different members of the beluga population in an attempt to surrogate the calf. ATL was ultimately hand-reared by the training and zoological staff but was consistently housed with the entire beluga population, including her biological mother.

Measures

The duration and frequency of four behavioral categories were coded for each archived, videotaped observation session: mother-calf swims, independent swims, social interactions, and allocare behaviors. Mother-calf swim involved a synchronized swim between mother and calf within 5 meters of each other[1]. Independent swim was defined by the calf swimming separately and asynchronously from the mother. Independent swims usually involved swimming in a trajectory that was different from the mother. Social interactions included any event in which the calf changed its behavior to join another animal to engage in play, mimicry of the other animal, or swim with a similar-aged peer. Allocare was any type of care of a calf performed by an adult beluga other than its mother. Although allocare events can include a broad range of behaviors, we limited our definition to behaviors that clearly cost the allocare provider: (a) synchronous pair swims between a calf and non-maternal adult in which the calf was within 5 m of the other adult and the calf was in an infant or an echelon position (an energy costly position for the adult carrying the calf along, Noren, Bidenbach, & Redfern, 2008; Noren & Edwards, 2011; Weihs, 2004), (b) the calf nursed from the adult female (metabolically demanding and energy costly, Amundin, 1986; Cheal & Gales, 1991, 1992), or (c) the adult retrieved or protected the calf (e.g., adult initiated a reunion when the calf was separated from its mother or threatened an animal approaching the calf, Mann & Smuts, 1998). This restrictive set of behaviors excluded interactions between the calf and other adult that might constitute a broader affiliative interaction that was not necessarily costly to the allocare provider. The initiator and receiver of each behavior were also recorded to assess the importance of this factor in allocare interactions. The initiator was the animal starting an interaction. The receiver was the recipient of the initiated interaction. In the event that an initiator was unidentifiable, it was marked as ambiguous and excluded from analyses in which initiator was assessed.

Procedure

Archived video recordings were used for the current study. All video recordings were collected using 15-minute focal follows for each mother-calf pair, two to three times a week for the first year of life for all five mother-calf pairs. All observation sessions were conducted in the absence of training staff to capture spontaneous behavior and minimize trainer influence. Each pair was recorded as a unique focal observation to ensure independence of observations. The observation orders were randomized and occurred once a day during operating hours between the hours of 0700 and 1800.

A total of 352 independent video sessions were viewed and coded by one coder (C. Campbell). Each video was coded in its entirety for its total length in seconds, the duration of each behavioral category of interest, the sequence of each behavioral category, and the initiating and receiving animals involved. If nursing occurred it was noted as an allocare event only and not timed, as this behavior is very difficult to observe reliably from video footage collected above water. If nursing occurred during a pair swim with an allocare provider, then the nursing was included in the overall duration of the pair swim. Finally, all periods during which the animals were not visible were timed and removed from the total video duration, so that all analyses were conducted with footage in which the animals were visible. Animals were considered not visible when they left the visual field or were occluded by an object longer than 3 seconds and/or displayed a behavior different from the behavior they were performing when they moved into a non-visible category. Only the behaviors of the focal pair were coded, unless one of the focal animals was involved in an interaction with another whale.

Coding reliability was assessed for 25 randomly selected videos in which allocare events occurred. A second independent coder, who was naïve to the purpose of the study, coded these videos. The two coders had 97% agreement on the frequency of allocare with two disagreements. These two disagreements were resolved by H. Hill. Finally, both coders were in 100% agreement on the initiator and receiver of agreed-upon allocare events.

Results

Activity Budget

A total of 80.8 hours comprised the data available for five mother-calf beluga pairs during their first year of life. Sixty allocare events occurred across this group of belugas, which accounted for 1.7% (1.4 hours) of the total visible observation time (Figure 2). As summarized in Table 2, two of the five calves were involved in the 97% of these events (QIN accounted for 55% of the allocare events and BEL for 42%) while OLI and ATL were equally represented in the remaining 3% of the allocare events. Mother-calf swim

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[1] This distance was selected as the maximum distance between swim partners to accommodate the various dimensions of the pools in which that the belugas were housed. This distance is equivalent to approximately two adult body lengths and was generally the maximum distance at which belugas in a synchronized pair swim swam.

accounted for 32.0% (25.9 hours), calf independent swims, 17.6% (14.2 hours), and social interactions, 2.4% (1.9 hours) of the visible time recorded across the first year of life for all five calves (Figure 2). The remaining visible time included behavioral categories that were not coded for this study (e.g., separations, reunions, and solitary play behaviors).
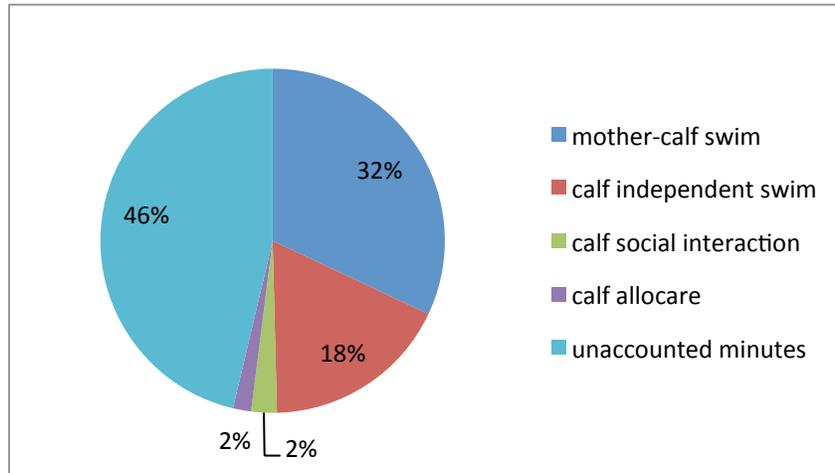
Figure 2. Percentage breakdown of time recorded in allocare events compared to time in other calf behaviors

Table 2. *Descriptives of the duration (sec) of behaviors of interest for calves and allomothers.*

	Mother-calf swim		Solo swim		Social interaction		Allocare	
	M	SEM	M	SEM	M	SEM	M	SEM
OLI	421.00	54.32	99.98	1.91	25.98	1.31	16.00[a]	---
GRA	356.69	5.51	112.15	2.58	22.38	0.93	---	---
QIN	91.25	0.39	38.90	0.14	3.52	0.05	105.27[b]	30.67
BEL	62.31	0.37	39.14	0.19	8.99	0.07	72.95[c]	16.39
ATL	--	--					35.00[d]	---
LUN							81.60[e]	24.37
WHI							49.17[f]	19.11

Note. Allocare means include observations in which only allocare occurred ($N = 60$). All other means include the entire data set.
[a] OLI received 1 allocare interaction from MAR.
[b] QIN initiated 19 allocare interactions with LUN and 3 allocare interactions with WHI.
[c] BEL initiated 20 allocare interactions with WHI.
[d] CRI & BEL initiated 1 allocare interaction with ATL.
[e] LUN initiated 10 allocare interactions with QIN.
[f] WHI initiated 1 allocare interaction with QIN and 5 allocare interactions with BEL.

Characteristics and Initiators of Allocare Events

Allocare events were restricted to three very specific types of behavioral events: swims between a calf and a female other than the mother, involving only infant or echelon positions, retrievals of the calf by the female other than the mother, and nursing bouts with the female other than the mother. Using the above limitations, only one calf, GRA, did not receive any allocare by an adult beluga during his first year of life. Of the calves receiving allocare, OLI was retrieved by and pair swam with MAR once at two days old, or a day before the birth of MAR's calf, GRA. Although these two mother-calf pairs (TIN-OLI and MAR-GRA) were housed with only each other during their first 10 months of life, no other allocare events were captured or observed for OLI or GRA during their first year of life even after they returned to the larger beluga group. The other single case of attempted allocare occurred between the female calf, ATL and the mother-calf pair,

CRI-BEL. Even though ATL and her mother, LUN, were housed with other adult females both with and without calves, ATL experienced only one attempt of allocare, initiated by CRI and BEL. When ATL was almost a week old and swimming independently from her mother, CRI and BEL attempted to initiate a swim with ATL, but ATL did not respond to their initiation attempt.

Finally, the majority of the allocare events observed in the video recordings involved the remaining female calves, QIN (N = 33 allocare events) and BEL (N = 25 allocare events). Born a year apart, both calves were housed with a variety of adult female belugas with and without calves. In particular, both calves had regular access to two adult females without calves, WHI and LUN. As summarized in Table 2, QIN engaged in 87.9% (N = 29) of her allocare events with LUN, an unrelated female, and initiated 65.5% (N = 19) of those events. QIN also received 10 allocare events from LUN and a single event from WHI. In contrast, BEL engaged in 80% (N = 20) of her allocare events with WHI, her biological sister, and initiated 100% of those events. Finally, BEL's remaining 20% of allocare events were initiated by LUN.

Comparison of Mother-Calf Interactions to All Other Behaviors

A series of dependent t-tests with a Bonferroni correction for multiple analyses was performed to compare the duration of mother-calf swims to the duration of each major behavioral category of interest: calf independent swims, calf social interactions, and allocare events. As expected, mother-calf swims were significantly longer than all other categories of interest (Figure 3). When compared to calf independent swims, mother-calf swims (M = 112.72 sec, SD = 247.35 sec) were about 4.5 times longer than the calf's independent swims (M = 50.62 sec, SD = 119.44 sec) during the first year, dependent $t(1302)$ = 7.92, p < 0.001. Likewise, when compared to social interactions involving the calf, mother-calf swims were more than 15 times longer in duration than the calf's other social interactions (M = 7.38 sec, SD = 36.12 sec), dependent $t(1302)$ = 15.13, p < 0.001. Finally, when compared to allocare interactions, mother-calf swims lasted four times longer than the allocare interactions (M = 3.80 sec, SD = 27.93 sec), dependent $t(1302)$ = 15.69, p < 0.001. Table 2 summarizes the means and standard deviations for each beluga.

An independent t-test was performed to determine if the length of the allocare event depended on whether a calf or an adult initiated it. The result indicated that the allocare event did not differ significantly in duration based on the age of the initiator (calf: M = 89.88 sec, SD = 115.57 sec; adult: M = 69.44 sec, SD = 67.51 sec). Similarly, a separate independent t-test indicated that QIN and BEL participated in similar length allocare events (Table 2 and Figure 4).

Discussion

The purpose of this exploratory study was to examine the frequency and nature of allocare events in a breeding group of belugas in human care during the first year of life. Over a period of four years, five beluga calves were observed through their first year of life. Four of those five calves were reared by their mothers, which included two primiparous mothers and two multiparous mothers. The fifth calf was hand-raised as she and her primiparous mother did not bond. All beluga pairs, except for the first two calves during the first 10 months of life, were housed with four to eight belugas by the end of their first year of life. The other belugas within this social group included adult females with and without calves and one of two adult males.
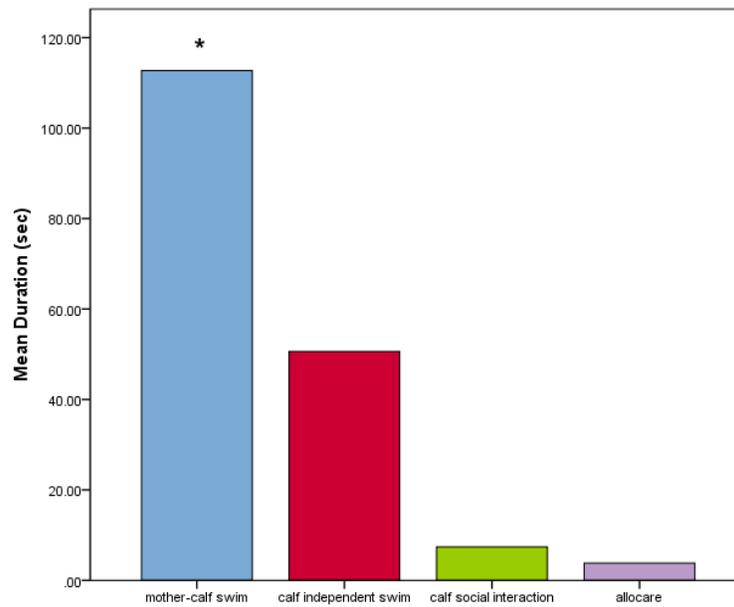
Figure 3. Mean duration of each behavior of interest. Mother-calf swims lasted significantly longer than all other swims, $p < 0.05$.
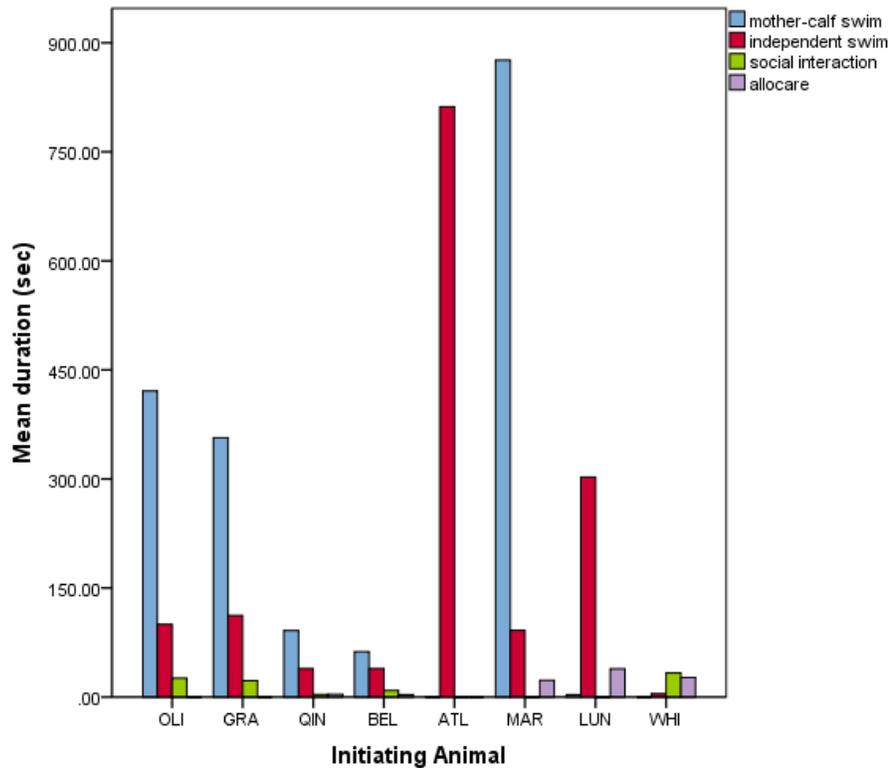
Figure 4. Mean duration of each behavior of interest for each calf and each adult involved in allocare. All calves (OLI to ATL) are represented and grouped oldest to youngest. Only the adults participating in allocare events are included (MAR to WHI). Note that the allocare bars (purple) are about equal in length indicating that there was no sigificant difference in duration of allocare events whether initiated by a calf or an adult.

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Frequency of Allocare

Allocare interactions occurred infrequently (a little less than 2% of the available visible time of the 80 hrs of independent video footage), as compared to other types of interactions involving the beluga calves during the first year of life. Although some scientists have suggested that allocare, particularly allonursing, may be an artifact of captivity due to the close proximity of females with and without offspring (Packer et al., 1992), the results of this study and others call this interpretation into question. Several studies, including the current one, indicated that while allonursing and other forms of allocare were exhibited by belugas in human care it did not occur simply because females without offspring were in close proximity to the calves as not all females allowed the calves to nurse from them (Leung et al., 2010; Whitehead & Mann, 2000; Winhall, 2012). Moreover, cases of allocare by belugas in their natural habitats have been observed (Krasnova et al., 2006, 2009). Like other animals displaying allocare (reviewed by Komdeur, 2006), access to adult females without calves alone was likely not the primary factor in determining the use of allocare by these belugas, despite the findings of Packer et al (1992). Rather, having access to whales of different ages without dependent offspring, recognizing that a young conspecific has a need for care, being motivated to care for another conspecific's offspring, and having a willingness to provide the necessary care are all factors that should be considered when examining possible factors of allocare.

Factors that May Influence Allocare by Belugas in Human Care

While the purpose of this study was not to test directly the influence of each variable on the likelihood of allocare by belugas, the results do provide some insight into which factors may play a role for this beluga group. First, the frequency of allocare clearly differed between the five calves. Within the first days of birth, the first male calf was retrieved by the second pregnant female beluga while swimming alone at a distance greater than five meters from his mother. The pregnant female swam with the calf for a short duration until his mother retrieved him. Following this initial allocare event, the first two calves were never observed in any other allocare event, despite being in close proximity with each other. Either allocare occurred but was not captured by the observations, or allocare was not necessary as both calves were monitored by their own mothers during interactions with each other or others once housed with the full beluga population (Hill, 2009).

The low frequency of allocare events may also be attributed to the absence of several factors, which have been associated with the presence of allocare (Packer et al., 1992). First, with the exception of the initial allocare event while the second female was still pregnant, the two mother-calf pairs were not housed with any females without calves for the first 10 months of life. Second, their housing environment had few potential threats to the calves (e.g., no predators, a limited number of social interactions that could become agonistic), which may have not produced many contexts in which the calves needed interventions from an animal other than their mothers. Third, both mothers monitored their calves' activities and likely did not require assistance from each other as their calves matured during the first year (Hill, 2009). The absence of these factors during early infancy may have precluded the need for allocare for these two calves even after they were integrated with the rest of the belugas.

Additional knowledge is provided by the case study involving the female calf that did not bond with her mother. This calf was raised in a very different environment from the first two male calves. In particular, she had access to several adult females that could have potentially provided various types of allocare, including long-term surrogate care. Once again, simple proximity was not sufficient to induce allocare efforts by any beluga as this calf did not reciprocate any social interactions initiated by other belugas, including the single attempt of allocare directed toward her by a beluga mother and her yearling calf. Ultimately hand-reared, this calf was never observed to nurse from or swim with any adult beluga

during this first year of life. This case study suggests the importance of both the adult and the calf in initiating, responding to, and maintaining any kind of interaction, including allocare behaviors.

In marked contrast, the two remaining female calves presented very different trends in their allocare. Like the two male calves, these females bonded with their mothers. However, unlike the male calves, these females had access to a variety of social compositions that included multiple adult females without calves as well as other mother-calf pairs. These conditions may have facilitated the display of allocare as both calves were retrieved by, swam with (i.e., echelon or infant position), or attempted to nurse from two young adult females without calves. Although the very strict definition of allocare implemented in this study possibly limited the frequency with which allocare was identified, it allowed us to eliminate any calf-other adult interactions that may have been more affiliative in nature (e.g., a social swim or play interaction). Thus, the identified allocare events in the current study should be considered as direct investment behaviors as they both altered the behavior of each caregiver at an energetic cost (Riedman, 1982; Trivers, 1981; Woodroffe & Vincent, 1994, Whitehead, 1995, 1996; Whitehead & Mann, 2000).

Individual Preferences

One point of interest was the individual preferences displayed by each calf and allocare provider. Both female calves tended to preferentially swim with or attempted to nurse from one of the two young adult females. QIN and LUN preferred each other during allocare interactions (88% of QIN's allocare interactions), while BEL and WHI preferred each other (80% of BEL's allocare interactions). Although both calves had access to both females and both females initiated allocare events with both calves, it is possible that different mechanisms may have driven the preferences observed. The preference observed between QIN and LUN may reflect reciprocal altruism (Riedman, 1982; Trivers, 1981), if LUN was preparing for help from SIK with her own future calf. However, it is also possible that LUN's willingness to care for the two calves may have been due to an attraction to young calves (Mann & Smuts, 1998). While either of these explanations may also be applied to BEL and WHI, one additional explanation is also possible: a kin-based interaction as WHI was BEL's older half-sister. Kin-driven allocare has been supported by many studies with mammals (Komdeur, 2006; Riedman, 1982; Schubert et al., 2009), including a population of sperm whales (Gero et al., 2009).

Additional explanations for the preferred partners include chance or previously established associations between the two adult females (e.g., LUN and SIK, QIN's mother or WHI and CRI, BEL's mother), however, only the previously established relationship between WHI and CRI is viable given that CRI was also WHI's mother. Using observations collected prior to the birth of either calf in this study, these observations did not indicate that LUN and SIK or CRI and WHI preferred one another as swim partners. Rather, all females acted independently of each other, pre-parturition (H. Hill, personal communication). As an exploratory study with a limited sample of belugas in a controlled environment, this study is only able to offer possible interpretations as opposed to clear explanations. Thus, a larger sample, including belugas in controlled habitats and their natural habitats, is needed to elucidate these mechanisms.

Another trend observed was the difference in the frequency of allocare experienced by the male calves versus the female calves. Parental investment theory (Trivers, 1972) or its extension, the Trivers–Willard hypothesis (Trivers & Williard, 1973) generally suggest that parents may bias their investment, or allocate resources, to one sex or the other depending on contextual factors, such as food availability or larger and stronger offspring (Trivers, 1972; Trivers & Williard, 1973). While a recent study with wild killer whales (*Orcinus orca*) suggested that the presence of post-menopausal mothers facilitated their male offspring's longevity (Foster et al., 2012) and thereby provided support for parental investment theory, the data from the current study are too limited to apply this explanation. First, belugas have a different social

structure than killer whales, which may have implications for parental investment (Kokko & Jennions, 2008; Schuster et al., 2009; Trivers, 1972). Unlike killer whales, which maintain a very dominant, matrilineal-based hierarchy (Baird, 2000; Foster et al., 2012), belugas seem to have a greater degree of flexibility in their social structure as compared to some bottlenose dolphin populations, like in Monkey Mia/Shark Bay or Sarasota Bay, Florida (Connor, Wells, Mann, & Read, 2000; Whitehead & Mann, 2000). Second, all the mothers in this study varied in their degree of vigilance over their calves' activities while also differing in their social compositions during the first year of life for each calf (Hill, 2009; Hill, Campbell, Dalton, & Osborn, 2013). These context-specific factors may have been more influential in this study than the proximate mechanism offered by the parental investment theory (Trivers, 1972; Trivers & Willard, 1973). Only long-term studies of belugas in both controlled and natural habitats will clarify if sex-biased parental investment strategies are used by belugas.

Initiator of Allocare: Mother, Calf, or Allomother?

Previous research on allocare in animals rarely discusses the initiator and receiver of allocare events as the allocare provider or the parental caregiver is perhaps assumed to initiate the allocare and the offspring are the receivers. While this may be true for altricial species, this may not necessarily be the case for precocial species. Previous studies with cetaceans failed to report on the initiating and receiving animal of allocare interactions (Gero et al., 2009; Leung et al., 2010; Mann & Smuts, 1998), possibly because of the difficulty in observing and recording these relatively rare events. One might assume that the mother takes her calf to an available female or the available female retrieves the calf to initiate an allocare event. However, the observations in the current study questioned this assumption as the two female calves initiated their allocare interactions more often than the adult females (their mothers or allomothers) initiated with them. Despite this difference in the frequency of initiated allocare interactions, whether it was calf-initiated or adult-initiated, the allocare-based swims lasted the same length, suggesting that the initiating animal did not influence the outcome of the interaction itself. Moreover, when compared to mother-calf swims, allocare interactions were significantly shorter in duration. These observations suggest that the allocare events did not replace the bond formed between the beluga calves and their mothers (Hill, 2009; Hill et al., 2013; Krasnova et al., 2006, 2009).

In summary, allocare events may serve several functions for belugas in controlled settings. First, allocare may provide an opportunity for adult females without calves to practice caregiving behaviors (Mann & Smuts, 1998; as reviewed by Whitehead & Mann, 2000). Second, allocare may provide "safe" opportunities for calves to develop independence from their mothers as the calves are received by and cared for by another beluga (Krasnova et al., 2006, 2009). Third, allocare may provide opportunities for mothers to rest without actively monitoring their calves (Gero et al., 2009; Whitehead, 1996). Finally, allocare may provide opportunities for calves to supplement their own energy stores as they draft from another adult while swimming or nurse from females besides their mothers (Leung et al., 2010; Packer et al., 1992).

Given that allocare occurred rarely in this population of belugas suggests that allocare in a controlled environment may not be needed as often as in a natural habitat, despite the interpretation by Packer et al. (1992) that a controlled environment artificially increases the frequency of allonursing. Perhaps, the advantages of controlled environments (better visibility, control over the environment, such as social compositions and limited threats to survival, detailed records of life history and health status) allow for more opportunities to observe the allonursing occurring as opposed to observing animals in their natural habitats. Alternatively, allocare may be more likely to occur spontaneously if the composition of a social grouping confers an advantage to the mother. For example, a cetacean mother in human care may be able to rest fully while her calf is cared for by another female as the mother could reduce her degree of vigilance over her calf (Lyamin, Pryaslova, Lance, & Siegel, 2005; Hill, Greer, Solangi, & Kuczaj, 2007). Thus, the development

of calves and their care as well as the maternal care skills of primiparous females may be facilitated by facilities that maintain naturalistic social groupings and house juvenile, sub-adult, or young adult females with mother-calf pairs. For example, adult females may be more likely to initiate or allow an allocare interaction initiated by a calf, if they do not have a calf of their own. Although we did not observe any allocare interactions involving an adult male beluga, and male cetaceans do not typically care for calves directly, male dolphins have been observed to provide direct forms of care to calves (Byerly et al., 2009; K. Dudzinski, personal communication). These observations suggest that given the appropriate circumstances, the survival of calves is dependent not just upon the maternal care received but also on the network of available social support (Stanton & Mann, 2012). Additional data on the frequency and nature of allocare in belugas and other cetaceans both in their natural habitat and in human care would offer insight into the role of allocare in calf survival.

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