



Individual differences in the behavioral characteristics of beluga whales (*Delphinapterus leucas*)



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ABSTRACT

The topic of individual differences in animal behavior has garnered a great deal of recent attention across many species, but questions remain concerning the degree to which behavioral differences vary over time or by age and sex. The present study focused on white whales (*Delphinapterus leucas*), a species in which a high degree of behavioral variability may be expected due to the fact that belugas are large-brained, long-lived, and highly social in nature. A suite of 23 behavioral measures related to boldness, playfulness, sociability, and other traits were assessed in 41 seaquarium-based belugas that were housed in mixed age/sex grouping. The goals were to assess consistency within individuals over time as well as variations by age and sex. Nineteen of the 23 measures showed significant within-subject consistency over time, suggesting that stable behavioral differences appear to exist in this species. However, very few measures showed significant correlations with each other, indicating that they could not be grouped into identifiable factors that comprised recognizable clusters. It is suggested, therefore, that individual differences are best viewed as a complex array of characteristics that depend on an individual's age and contextual variables that influence the degree to which specific sets of behaviors are expressed and co-vary.

1. Introduction

The topic of individual differences in the behavioral characteristics of non-human animals has garnered a recent surge in attention in the scientific literature (Hill et al., 2017a, 2017b). Sexual selection, foraging adaptations, ecological specializations have all been posed as lifespan domains in which the selection of stable individual variation across time and context would be adaptive (e.g., Dall et al., 2012; Dingemans and Réale, 2005; Smith and Blumstein, 2008). Functionally, natural selection may favor stable differences among individuals by producing advantageous fitness consequences. In this regard, a meta-analysis conducted by Smith and Blumstein (2008) found evidence that higher levels of exploration were associated with slight increases in survival, and higher levels of aggression were associated with increased reproductive fitness across the species examined.

Studies of individual differences in non-human animals have utilized one of three types of measurement: 1) human ratings of specific adjectives that are thought to reflect an aspect of a trait, 2) ratings of behaviors that are categorized on a Likert scale, or 3) direct observations of spontaneous behavior (Vazire et al., 2007). While all three types of measurements appear to be used reliably in some contexts,

convergent validity has been difficult to attain across contexts and over time (reviewed in Uher and Asendorpf, 2008). Reasons for the difficulty in attaining reliability across these measures may include the origin of definitions, as well as variation in human-based contexts and in the natural, spontaneous behavior of the animals themselves, such as expressions at different life stages, across seasons, or over time (Carere et al., 2005; David et al., 2012; Günther et al., 2014; Svartberg et al., 2005).

Inconsistent outcomes may also stem from the variety of terms used to describe various aspects of individual differences in animals (reviewed by Stamps and Groothuis, 2010 and Hill et al., 2017a, 2017b). Two common terms in the literature on individual differences include behavioral syndrome and personality. Whereas the term behavioral syndrome has been used most frequently to refer to behaviors that are stable across contexts OR across time, the term personality has been most often used to refer to behaviors and/or traits that are stable across contexts AND across time. The result has been a “somewhat haphazard” focus on species within specific contexts or time. Few studies have attempted to assess the convergent validity of measures by assessing individual differences in the spontaneous behavior exhibited by animals, human ratings of characteristics, and human ratings of behaviors in the

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same subjects (Uher & Asendorf, 2008). These oversights have led to mixed results and ambiguous interpretations of personality or behavioral syndromes (reviewed by Stamp and Groothuis, 2010).

Delphinids (e.g., bottlenose dolphins) and pinnipeds (e.g., sea lions, seals) have been the primary subjects of individual differences research for marine mammals (Ciardelli et al., 2017; de Vere et al., 2017; Highfill and Kuczaj, 2007; Kuczaj and Eskelinen, 2014; Kuczaj et al., 2012a, 2012b). However, the assessment of individual differences in marine mammals are good examples of the limitations reviewed above, in that most such studies have been limited to the use of ratings of characteristics or traits (de Vere et al., 2017; Kuczaj and Eskelinen, 2014; Highfill and Kuczaj, 2007; Kuczaj et al., 2012a, 2012b). To compound the issue, the majority of these studies were limited to one period of time and thus did not include an assessment of temporal consistency (exception, Highfill and Kuczaj, 2007).

Bottlenose dolphins (*Tursiops truncatus*) have been the primary subjects with results indicating that human ratings of dolphins can be consistent across raters and over time. To date, individual differences have been reported for specific behaviors, including pectoral fin contact (Dudzinski et al., 2012) and responses to familiar and unfamiliar stimuli or preferences for specific environmental enrichment devices by dolphins (Delfour and Beyer, 2012; Eskelinen et al., 2015; Yeater et al., 2014). Only one study evaluated the consistency of dolphin traits, using adjective-based, trainer ratings over an almost two-year period that also included a major environmental catastrophe and a relocation (Highfill and Kuczaj, 2007). The results of that study suggested that out of 14 dolphins, 12 adult females remained consistent in their ratings across all five personality traits from before the environmental catastrophe to after when housed at a new facility. The majority of the dolphins did display variation in some of their traits, suggesting that context was critical, or that time and/or experience may have had a significant effect on individual differences in behavior. Much less is known about the stability of individual differences in other cetaceans.

It can be argued that belugas (*Delphinapterus leucas*) are good candidates for research of this type. They are whales that inhabit Arctic waters near the edge of polar ice, and like delphinids, belugas are long-lived, large-brained, and highly gregarious, with evidence of cultural transmission in their migratory routes and foraging traditions (O'Corry-Crowe et al., 2018). Such traits appear to be associated with high degrees of variability in behaviors and dispositions across individuals, as many of the species displaying evidence of behavioral syndromes or personality share these characteristics (reviewed in Stamps and Groothuis, 2010 and Hill et al., 2017a, 2017b).

Thus, in order to provide data on individual differences in a new species of cetacea, the present study examined the consistency over time of 23 behavioral measures in a population of seaquarium-based beluga whales, and the degree to which these measures correlated with one another. It was expected that individual differences would be consistent over time. Additionally, it was expected that there would be a pattern of correlations among the multiple measures that would be consistent with the notion of behavioral syndromes reported in other species.

2. Method

2.1. Subjects

The subjects of this investigation were 41 beluga whales housed at Marineland of Canada (Niagara Falls, Ontario). Twenty-one adults (4 male, 17 female) had previously been wild caught in the Chuchki Sea, and were estimated to range from 11 to 25 years of age. An additional 20 belugas (7 males, 13 females) had been born at Marineland, and ranged in age from 1.5 to 14 years. Over the three-year period of this investigation, the whales were housed in mixed-sex, mixed-age groupings in three separate pools ranging in size from 5 to 9 million liters (see Table 1).

2.2. Procedure

Twenty-three behavioral traits were observed using four observational paradigms over several time periods. Fourteen measures derived from direct observations of the belugas' behaviors by trained research assistants. Some measures consisted of repeated ratings that were averaged to produce single scores for each observation session (for example, swim depth was recorded in behavioral scans (2–3 scans per 30 min observation) then averaged for a single session measure). Others were proportions of the number of affirmative sample points collected by the observer on a given observation day. Finally, several measures were percentages or rates of specific behaviors as measured directly with all occurrence recording (e.g., all play behaviors). The operational definitions pertinent to each behavioral assessment is specified in columns 2–5 of Table 2. Ratings of nine traits were also collected from the marine-mammal trainers who had worked with individual whales for at least five years. The trainers rated specific traits on a 10-pt Likert scale (0 – low frequency of observed trait to 10 – high frequency of observed trait). For these trainer surveys, adjectives were selected to correspond to use in other studies (de Vere et al., 2017; Highfill and Kuczaj, 2007; Kuczaj et al., 2012a, 2012b; Vazire et al., 2007), and to the behavioral measures in this study. The trainers were given no instructions other than to rate each whale on each adjective.

2.3. Statistical analyses

Intraclass correlations were conducted to assess stability over time. Pearson correlation coefficients were calculated to assess associations across behavioral measures, (and inter-observer reliability where applicable). In order to minimize familywise error when assessing associations across behavioral measures, only correlations with a *p* value of .005 or lower were considered significant. Two-way analyses of variance (ANOVAs) were used to examine sex and age differences for each behavior/trait. Preliminary analyses conducted to determine if birth setting (wild vs captivity) affected any of the variables indicated no differences between the two birth settings.

3. Results

3.1. Within-subject consistency across time

Of the 23 behaviors assessed in this investigation, 19 showed evidence of within-subject consistency across time (specific results provided in Reliability column of Table 2). As the data were collected over different time frames, the results are organized by temporal spans:

3.1.1. Across four months

Significant intraclass correlations (ICC) ranging between .52 to .69, were observed for five of the seven behaviors measured across four consecutive months (grey shading in Table 2). These measures included characteristics of the ways in which the whales swam, and their closeness to the observation windows.

3.1.2. Across eight months

The direction in which each whale circled the pool (or, perhaps more accurately, the extent to which each whale deviated from the predominant leftward circling) showed a very strong consistency from one Spring to the subsequent Autumn (ICC = .87).

3.1.3. Across years

Significant intraclass correlations, ranging between .32 and .55, were obtained for four of the six behaviors assessed across consecutive years (Table 2). Three of these pertain to different assessments of play behavior. The fourth reflected individual differences in the tendency to look at novel enrichment objects.

Table 1
Number of subjects, as a function of sex, age, year and pool.

	Pool 1 (9 million l)				Pool 2 (5 million l)				Pool 3 (5 million l)			
	0–6 yrs		7–25 yrs		0–6 yrs		7–25 yrs		0–6 yrs		7–25 yrs	
	M	F	M	F	M	F	M	F	M	F	M	F
Year 1	0	3	4	2	3	5	2	9	2	4	0	8
Year 2	2	5	4	3	1	1	0	7	2	5	2	10
Year 3	2	4	4	3	5	2	0	9	2	3	2	10

3.2. Trainer ratings

Significant interrater reliability among trainers was obtained for eight of the nine trainer ratings, ranging between .42 and .77 (Table 2).

3.3. Inter-measure correlations

When a correlation matrix was computed comparing each of the 23 measures with the others, only 32 of the 253 unique pairwise comparisons reached statistical significance. Only the significant findings are presented in Table 3, which includes the correlations that occurred among the measures of observed behaviors and the ratings by trainers.

3.4. Sex and age differences

The results of two-way ANOVAs that assessed the degree to which the traits varied across age and sex is summarized in the last two columns of Table 2. Age differences did emerge for several measures. Adult whales were significantly more likely to swim in non-standard body orientations, to display vigilant behavior, and to be rated as dominant. Immature whales were rated by trainers as more spontaneous and more likely to be at the observation window. On the other hand, significant sex differences were not found for any measure. Likewise, there were no significant interactions between age and sex for any behaviors measured.

4. Discussion

The results of this mixed-methods study indicate that belugas in managed care display consistent, individual differences. Inter-observer and/or inter-rater reliability were strong for most measures, suggesting that the behaviors were clearly recognizable and consistently rated. Out of 23 behavioral measures, 19 showed significant within-subject consistency over time. Both of these findings strongly suggest that the population of mixed age and sex belugas in this study exhibited evidence of behavioral syndromes (Stamps and Groothuis, 2010).

Somewhat surprisingly most of the measures did not cluster significantly with each other. Most of the exceptions involved play. The almost perfect relationship between total play and solitary play reflected the fact that solitary play was the most common form of play observed. Solitary play was also positively correlated with social play and sociability of the whales, suggesting that playing independently was related to playing with others and being near other whales. All of the above play behaviors were also positively correlated with the degree of time the whales were present at the human observation windows. Play with humans was also positively correlated with social play.

Total play behavior positively correlated with sociability, which may be represented as a crowd behavior combined with stimulus enhancement (Kuczaj et al., 2012a, 2012b; Yeater and Kuczaj, 2010). That is, as one animal attended the object other animals were drawn over and remained in close proximity to the animal interacting with object. The relationship between first to look at an enrichment object and first to touch may represent two separate factors: curiosity and investigation (boldness), respectively. This proposed hypothesis could be indirectly

supported by the positive correlation between playfulness and time spent at the window or degree of engagement with a human. Collectively, the belugas' responses to the novel object, to humans in the underwater viewing window, and the proportion of time spent at the window in general may represent different contexts in which individual variability in playfulness appeared to emerge, and since these behaviors were measured over different time points, it is possible that this category of behavior could be classified as a trait of personality (as explained in Stamps and Groothuis, 2010). Future research is needed to disentangle and clarify this explanation.

The significant correlation between the tendency to swim in non-dorsal body orientations and not swimming in the typical counter-clockwise direction indicated that whales that were most often observed to swim in an unusual pattern in one way tended to be the same whales that also swam in an unusual pattern in another way. These departures from the typically expressed behaviors could reflect differences in an individual characteristic of originality inherent to the openness factor of the Big Five Model of personality developed by Costa and McRae (as reviewed by Fürst et al., 2016). Additional measures of spontaneous behavior reflecting originality should be assessed to further explore this possibility.

Finally, it is interesting and somewhat problematic that the ratings by trainers using adjectives derived from human contexts were often correlated with each other while they did not correlate with the directly observed behaviors in this study. Overall, these correlations suggest that there was significant overlap between the constructs assessed by the trainers. It is possible that the traits were not well-defined, overlapped in construct, or the trainers may have had either different perceptions of the trait or different direct experiences with the whales, which influenced their ratings. Uher and Asendorpf (2008) summarized the difficulty previous studies had attaining convergent validity with similar types of measures. Those authors indicated that to assess behavioral variation validly behavioral measures across different contexts and times were needed as these parameters were the most accurate representations. However, the high degree of correspondence among the three trainers strongly suggests that the trainer ratings also reflected a reliable personality assessment (Kuczaj et al., 2012a, 2012b; Vazire et al., 2007). While the direct observation behaviors may be a more accurate representation of behaviors at any one time period, the trainers might provide a longer-term perspective. It will clearly take many years of diligent research effort to fully evaluate these distinctions (e.g., Stamps and Groothuis, 2010; Uher and Asendorpf, 2008). In any event, the present findings provide substantial evidence for beluga whale behavioral syndromes, thus enhancing our understanding of individuality in non-human animals.

Since the population of whales investigated in the present study included both sexes and a range of ages, it was possible to additionally examine differences by sex and age. Although no sex differences were found in this case, some age differences did emerge. Immature whales were rated as more spontaneous by the trainers, and more likely to be at the observation window as compared to adults. Adult whales, on the other hand, were more likely to swim in non-standard body orientations, and to touch a novel toy placed into their environment. Such age-based behavioral patterns correspond to similar finding in previous

Table 2
Description of behaviors assessed for stability over time and individual belugas and resulting statistics.

Name	Description	Frequency	Scale	Observer	Reliability	Year/Pool	Sex Differences	Age Differences
Across 4 months Average Swimming Speed	From scans, the average swimming speed across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0-5 (highest)	Direct Observation	First 2 mo vs second 2 mo ICC = 0.547, $p = 0.010$, 1-tail	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 0.533$, ns	$F(1) = 0.19$, ns
Average Swimming Depth	From scans, the average position in the water column across sessions.	8-28 30-min observation sessions, conducted 3x/wk	1 (touching bottom)-5 (touching surface)	Direct Observation	First 2 mo vs second 2 mo ICC = 0.519, $p = 0.015$, 1-tail	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 0.17$, ns	$F(1) = 1.67$, ns
Body Orientation	From scans, the proportion of occasions with a body orientation other than dorsal-upward across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0-100	Direct Observation	First 2 mo vs second 2 mo ICC = 0.694, $p = 0.001$, 1-tail	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 2.55$, ns	$F(1) = 4.25$, $p = 0.051$ Adults > Juveniles
Window-looking 1	From scans, the proportion of occasions in which the whale was close to and facing the underwater viewing window, across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0-1	Direct Observation	First 2 mo vs second 2 mo ICC = 0.674, $p = 0.002$, 1-tail	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 1.84$, ns	$F(1) = 0.78$, ns
Visibility	From scans, the proportion of occasions in which the whale was visible (i.e., whale was in the front 50% of the pool), across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0-1	Direct Observation	First 2 mo vs second 2 mo ICC = 0.519, $p = .007$, 1-tail	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 0.01$, ns	$F(1) = 0.96$, ns
Sociability	From scans, the proportion of occasions in which the whale was within one body length (approx. 3 m) of any other whale, across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0-1	Direct Observation	First 2 mo vs second 2 mo ICC = 0.378, ns	Year 2 Pools 1 & 2 (pool 2 adults only)	$F(1) = 1.17$, ns	$F(1) = 1.98$, ns
Arousal	From scans, the average of the perception of each whale's level of arousal, across sessions.	8-28 30-min observation sessions, conducted 3x/wk	0 (lowest)-4 (highest)	Direct Observation	First 2 mo vs second 2 mo ICC = 0.109, ns	Year 2 Pools 1 & 2	$F(1) = 0.67$, ns	$F(1) = 5.34$, $p < 0.5$. Adults > Juveniles
Across 8 months Swimming Direction	From focal follows, percent of total circuit swims around the pool that were leftward across observation sessions.	5-min observation sessions, conducted 3x/wk for 4 wks (12 observation days).	0-100	Direct Observation	Inter-rater reliability $r = 0.601$, $p < .001$ Spring vs Autumn ICC = 0.865, $p < .001$, 1-tail	Year 3 Pools 1 & 2 (adults only)	$F(1) = 0.42$, ns	Not applicable
Across years Playfulness Total	From all-occurrences observations, number of play events of any type per minute, across sessions.	10 30-min observation sessions conducted 3x/wk over 2 years. Total = 2090 min over 60 days.	Play events per minute	Direct Observation	Year to year correlation ICC = 0.524, $p = .004$, 1-tail	Years 1 & 2 Pools 1, 2, & 3	$F(1) = 0.61$, ns	$F(1) = 0.08$, ns
Playfulness Solo	From all-occurrences observations, number of solitary play events per minute, across sessions.	10 30-min observation sessions conducted 3x/wk over 2 years. Total = 2090 min over 60 days.	Play events per minute	Direct Observation	Year to year correlation ICC = 0.548, $p = .004$, 1-tail	Years 1 & 2 Pools 1, 2, & 3	$F(1) = 0.52$, ns	$F(1) = 0.07$, ns
Playfulness Social	From all-occurrences observations, number of social play events per minute, across sessions.	10 30-min observation sessions conducted 3x/wk over 2 years. Total = 2090 min over 60 days.	Play events per minute	Direct Observation	Year to year correlation ICC = 0.312, ns	Years 1 & 2 Pools 1, 2, & 3	$F(1) = 2.75$, ns	$F(1) = 0.15$, ns
Playfulness Human Directed	From all-occurrences observations, number of human-directed play events per minute, across sessions.	10 30-min observation sessions conducted 3x/wk over 2 years. Total = 2090 min over 60 days.	Play events per minute	Direct Observation	Year to year correlation ICC = 0.461, $p = .043$, 1-tail	Years 1 & 2 Pools 1, 2, & 3	$F(1) = 1.30$, ns	$F(1) = 0.41$, ns
First to Enrichment Object Look-At	From all-occurrences observations, following the introduction of an enrichment object, the number of times each whale approached and appeared to look at an artificial enrichment object, across sessions.	20-min observation periods conducted 3x/wk for a total of 10 days in each of 2 years	Events per minute	Direct Observation	Year to year correlation ICC = 0.352, $p = 0.042$, 1-tail	Years 2 & 3 Pools 1 & 3	$F(1) = 1.53$, ns	$F(1) = 2.93$, ns
First to Enrichment Object Touch	From all-occurrences observations, following the introduction of an enrichment object, the number of times each whale approached and touched an artificial enrichment object, across sessions.	20-min observation periods conducted 3x/wk for a total of 10 days in each of 2 years	Events per minute	Direct Observation	Year to year correlation ICC = 0.177, ns	Years 2 & 3 Pools 1 & 3	$F(1) = 0.37$, ns	$F(1) = 4.55$, $p < 0.05$ Adults > Juveniles

(continued on next page)

Table 2 (continued)

Name	Description	Frequency	Scale	Observer	Reliability	Year/Pool	Sex Differences	Age Differences
Trainer Ratings Window-looking 2	Ratings following five plus years of daily contact.	Based on daily viewing over most recent year.	0-100	Trainer Ratings	Trainer-trainer rs ranged btw 0.56 and 0.77, $p < .001$	Pools 1,2, & 3	$F(1) = 1.25$, ns	$F(1) = 7.27$, $p < 0.5$ Juveniles > Adults
Curiosity	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw 0.24 and 0.50, ns & $p < .01$, 1-tail, respectively	Pools 1,2, & 3	$F(1) = 0.97$, ns	$F(1) = 0.16$, ns
Boldness	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw 0.62 and 0.65, $p < .001$	Pools 1,2, & 3	$F(1) = 0.00$, ns	$F(1) = 1.73$, ns
Assertiveness	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw 0.58 and 0.60, $p < .001$	Pools 1,2, & 3	$F(1) = 0.18$, ns	$F(1) = 2.02$, ns
Spontaneity	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw -0.07 and 0.61, ns & $p < .001$, respectively	Pools 1,2, & 3	$F(1) = 0.00$, ns	$F(1) = 5.08$, $p < 0.5$ Juveniles > Adults
Dominance	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw 0.663 and 0.856, $p < .001$	Pools 1,2, & 3	$F(1) = 3.59$, ns	$F(1) = 22.99$, $p < 0.01$ Adults > Juveniles
Food Motivation	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw 0.50 and 0.71, $p < .001$	Pools 1,2, & 3	$F(1) = 0.22$, ns	$F(1) = 2.28$, ns
Tactile Motivation	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw -0.02 and 0.42, ns & $p < .01$, 1-tail, respectively	Pools 1,2, & 3	$F(1) = 1.64$, ns	$F(1) = 0.16$, ns
Trainer Motivation	Ratings following five plus years of daily contact.	Independent surveys of three trainers.	0-10	Trainer Ratings	Trainer-trainer rs ranged btw -0.02 and 0.28, ns	Pools 1,2, & 3	$F(1) = 0.85$, ns	$F(1) = 0.21$, ns

Note. Highlighted cells emphasize significant results. Unless specified, probabilities derive from two-tailed assessments.

Table 3
Significant correlations between behaviors/traits meeting p of .005 and below.

Category	Behavior/Trait 1	Behavior/Trait 2	r	p	
Direct Observations	Playfulness Total	Playfulness Solitary	.99	< .001	
	Playfulness Total	Playfulness Social	.55	< .001	
	Playfulness Total	Sociability	.59	< .001	
	Playfulness Solitary	Social play	.52	< .001	
	Playfulness Solitary	Sociability	.56	< .001	
	Playfulness Social	Sociability	.82	< .001	
	Playfulness Social	Playfulness-human	.74	< .001	
	Playfulness Social	Window looking 1	.46	.001	
	Playfulness Social	Window looking 2	.42	.003	
	Window looking 1	Window looking 2	.54	< .001	
	Window looking 1	Playfulness-human	.42	.003	
	Body Orientation	Swim Direction	-.64	.001	
	Trainer Ratings	Window looking 2	Curiosity	.63	< .001
		Window looking 2	Tactile motivation	.55	< .001
		Window looking 2	Spontaneity	.51	< .001
		Curiosity	Spontaneity	.63	< .001
		Curiosity	Boldness	.40	.004
Assertiveness		Boldness	.89	< .001	
Assertiveness		Food motivation	.67	< .001	
Assertiveness		Dominance	.63	< .001	
Assertiveness		Tactile motivation	.47	.001	
Assertiveness		Trainer motivation	.41	.004	
Boldness		Dominance	.57	< .001	
Food motivation		Boldness	.62	< .001	
Food motivation		Dominance	.55	< .001	
Trainer motivation		Spontaneity	.54	< .001	
Trainer motivation		Tactile motivation	.52	< .001	
Trainer motivation		Boldness	.43	.003	
Tactile motivation		Curiosity	.66	< .001	
Tactile motivation	Spontaneity	.54	< .001		
Tactile motivation	Boldness	.47	.001		
Dominance	First to look at enrichment object	.44	.005		

studies with other cetacean species (Gibson & Mann, 2008; Highfill and Kuczaj, 2007; Hill et al., 2017a, 2017b; Hill et al., 2008; Kuczaj et al., 2006, 2012a, 2012b; Lopes et al., 2016; Paulos et al., 2010). In the context of these belugas, immature whales have more experience to gain than adult belugas, which likely increases their engagement in spontaneous activities, such as looking at what is on the other side of their underwater window. In comparison, adult belugas provide protection for immature belugas, which may manifest in the behaviors reported above. Since such age differences indicate variations in behavioral characteristics over the lifespan, future studies should examine multi-year longitudinal data on behavioral trends to examine how juvenile behavior patterns shift into adulthood, and how individual characteristics mature across the lifespan. It is encouraging that a few studies have already begun to examine these questions in other species. The general finding is that temporal stability exists for some measures of personality but not all (Carere et al., 2005; David et al., 2012; Günther et al., 2014; Svartberg et al., 2005).

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