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## **Characterizing Curiosity-related Behavior in Bottlenose (*Tursiops truncatus*) and Rough-toothed (*Steno bredanensis*) Dolphins**

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Dolphins are frequently described as curious animals; however, there have been few systematic investigations of how dolphins behave when they are curious and the extent to which individual differences in curiosity exist in dolphins. Previous research has described individual differences in dolphins' frequency of interactions with environmental enrichment as well as quantifying curiosity-related traits of dolphins via personality assessments, though behavioral observation and trait rating components have not been part of the same study. The present study describes two different experiments designed to elicit curiosity in 15 bottlenose (*Tursiops truncatus*) and 6 rough-toothed (*Steno bredanensis*) dolphins. In Experiment 1, dolphins displayed more curiosity-related behavior toward a stimulus with spontaneous movement (jack-in-the box) compared to their reaction to a static control object; however, in Experiment 2, the subjects did not conform to hypotheses, and displayed few behavioral differences when shown expectation-violating stimuli compared to a control stimulus. The results of this study supported the hypothesis that there would be a wide range of individual differences in dolphins' reactions to the stimuli, including differences between species and sex, as well as differences in trait ratings by trainers. These findings provide information that may be useful for future research aimed at assessing curiosity in dolphins, as well as for making environmental enrichment decisions for dolphins in human care.

Dolphins are commonly described as very curious animals in non-scientific literature; however, the nature of dolphins' curiosity has not been well characterized by existing research. Although dolphins are often labeled as curious, some dolphins are more likely than others to explore and show interest in novel stimuli and some dolphins avoid novelty in their environment (Kuczaj, Highfill, & Byerly, 2012; Lopes, Borger-Turner, Eskelinen, & Kuczaj, 2016). A better understanding of dolphins' curiosity can allow for a better understanding of individual differences in dolphins, help with future behavioral and cognitive research on dolphins, and may inform decisions about provision of environmental enrichment.

Curiosity can be an adaptive trait that fosters creativity, innovation, and a better understanding of one's surroundings (Byrne, 2013; Kuczaj, 2017). Given the complex social and ecological environment of dolphins, curiosity is likely to be a beneficial trait for finding food and learning about other conspecifics. A general definition of curiosity is a trait-like disposition and a state of subjective uncertainty, both of which lead to exploratory behavior (Byman, 2005). Curiosity is distinct from boldness, because although a curious animal can act in a bold manner, curiosity involves information-seeking behavior that is more cognitive in nature than simply approaching a novel object (Byrne, 2013). Previous research on curiosity in animals has relied on observable behavioral indicators, such as exploration of new spaces or manipulation of novel objects (Glickman & Sroges, 1966). Birds, rats, non-human primates, and fish have all been the subject of research aimed at identifying personality traits, such as neophobia (fear of novelty) and neophilia (affinity for novelty), and placing individuals along the shy-bold continuum (Dellu, Mayo, Piazza, Le Moal, & Simon, 1993; Hughes, 1997; Wilson, Clark, Coleman, & Dearstyne, 1994). Though this past research has been beneficial for understanding individual differences, only measuring subjects' response to novelty fails to capture how individuals interact with objects that are no longer novel, as is the case after the first exposure. In this way,

neophilia is distinct from curiosity because individuals may display interest, engagement, or seek information about an item, even when that item is no longer novel.

Shyness and boldness are often discussed as one dimension of individual differences that can be possessed by humans and animals, where variation exists in an organism's tendency to seek novelty (Wilson et al., 1994). Within a population, it is beneficial to have some individuals who are willing to take risks with the benefit of finding new resources, while other individuals remain sheltered from novelty and possible danger (Wilson et al., 1994). Wilson et al. (1994) discussed several mechanisms for this variation including genetics, experience, and population density. Similar to examinations of boldness, examining curiosity in a variety of species can reveal important information about cognitive processes, survival strategies, and the types of information that are useful to a particular species (Byrne, 2013).

Kuczaj (2017) argued that curiosity is a catalyst for creativity and innovation in many species. The drive to explore and investigate stimuli and unfamiliar situations is what leads individuals to discover new foraging techniques or begin behavioral traditions. Furthermore, individual differences in curiosity within a species influence the behavioral diversity of individuals and other group members (Kuczaj, 2017). In particular, the "watchful cautious" animals may benefit most from the curiosity of group mates because they observe a bolder individual's interaction with some novelty while avoiding potential risks themselves. This behavior has been observed in dolphins, where some individuals hid behind others and looked over the bold individual's "shoulder" as they interacted with a novel device that produced bubble rings (Kuczaj, Yeater, & Highfill, 2012). These "watchful cautious" animals later interacted with the bubbles themselves, but they seemed to use the behavioral reactions from peers as cues to guide their own interactions. The "watchful cautious" individuals seemed to be curious about the device but were not necessarily bold when the device was first introduced, thus further illustrating the subtle differences between boldness, neophilia, and curiosity. Research on individual differences in curiosity is needed to assess the importance of this trait for the ability of individuals, social groups, and species to be innovative and creative (Kuczaj, 2017). For example, orangutans' problem solving ability is predicted by each individual's level of curiosity, as measured by their response to novelty and willingness to explore (Damerius, Graber, Willems, & van Schaik, 2017).

The introduction of novel stimuli is often used by zoological facilities to create a variable environment and reduce stereotypic behavior of animals. A study on the effects of environmental enrichment in mink found that while some individuals examined and manipulated novel objects placed in the habitat, other animals, who had previously exhibited more stereotypic behavior, became inactive and avoided the novelty (Dallaire, Meagher, & Mason, 2012). Additionally, zoological facilities often use the same objects repeatedly as enrichment items by presenting the items on a variable schedule, which has been shown to be effective for some species (Kuczaj, et al., 2002). Presentations of visual stimuli, most commonly using television screens, has been found to capture the attention of several species, including killer whales, rhesus monkeys, and shelter cats, and has thus been considered engaging (Ellis & Wells, 2008; Hanna, et al., 2017; Platt & Novak, 1997). Therefore, even when a stimulus is not novel and cannot be physically manipulated, many different species have exhibited sustained curiosity about, and engagement with visual displays.

The individual differences in the reactions of animals to enrichment items revealed by the above research indicate that it is important for zoological facilities to understand this variation, in order to best care for the animals. For example, dolphins have shown differences in the number of times each individual interacts with environmental enrichment and novel objects; however, these studies did not directly assess the specific behaviors associated with curiosity (Eskelinen, Winship, & Borger-Turner, 2015; Lopes et al., 2016). Dolphins in the wild and under human care have demonstrated an interest in natural and man-made objects. Overall,

young animals interact with environmental enrichment more often than older animals (Eskelinen et al., 2015; Greene, Melillo-Sweeting, & Dudzinski, 2011). In an analysis of sex differences, Eskelinen et al. (2015) found adult males in human care interact more with objects compared to females, while Greene et al. (2011) found wild adult males interact with objects less than wild females.

As of yet, no systematic behavioral observations have been conducted for cetaceans on measures of curiosity. Previous research on personality in bottlenose dolphins has relied upon ratings by humans familiar with the study subjects (Highfill & Kuczaj, 2007; Kuczaj, Highfill, et al., 2012). These ratings could be especially useful in making environmental enrichment decisions if they were validated with behavioral observations. Personality factors in chimpanzees have been corroborated with behavioral data collected by independent observers, supporting the predictive validity of ratings by caregivers (Freeman et al., 2013).

One reason animals may be curious about an external stimulus is that it is at least partially unfamiliar to them. Piaget (1952) described a similar situation with human infants as a “moderately discrepant” event because although part of the event is familiar to the individual, there is some aspect of it that is unfamiliar. Human infants begin integrating new information from the environment with their existing schemas at an early age and eventually test the properties of objects during play in order to better understand them (Piaget, 1952). Dolphins’ play is also reflective of the learning that Piaget described (Kuczaj & Eskelinen, 2014; Kuczaj, Makecha, Trone, Paulis, & Ramos, 2006). For example, when playing with bubbles, some dolphins modify their behavior in order to learn about the properties of the bubbles, highlighting the significance of play in cognitive development and knowledge acquisition.

Another research paradigm that can rely on the subject’s curiosity is called violation of expectations (VOE). This paradigm has been used in research with young children and several species of non-human animals to determine if an event is perceived as unexpected. In this paradigm, the length of time a subject spends looking at an event that violated expectations or exploring the object from the event is compared to the subject’s reaction to an event that does not violate expectations. The differences in behavior between the two conditions are indicative of what the subject finds interesting and understands about the world, as individuals are likely to have a longer gaze duration for an unexpected event (Hauser & Spaulding, 2006; Santos, Barnes, & Mahajan, 2005; Stahl & Feigenson, 2015). Information-seeking behavior, including longer gaze duration, which occurs following an unexpected event can therefore be indicative of curiosity.

Dolphins are able to discriminate between familiar and unfamiliar human individuals, as individual animals spend different amounts of time looking at humans who are unfamiliar versus familiar (Hill et al., 2016; Thieltges, Lemasson, Kuczaj, Böye, & Blois-Heulin, 2011). Bottlenose dolphins, Pacific white-sided dolphins, and beluga whales look longer at unfamiliar compared to familiar objects, which confirms that this behavior occurs in several cetacean species (Guarino, Yeater, Lacy, Dees, & Hill, 2017). Additionally, dolphins looked longer at a scenario that violated the property of object permanence compared to a scenario that did not violate this property, which suggests dolphins understand something about object permanence (Singer & Henderson, 2015). Previous research, using both gaze direction and active choice response, indicates that dolphins are able to track objects that have been occluded by a larger object (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010; Johnson, Sullivan, Buck, Trexel, & Scarpuzzi, 2014).

In addition to an increase in gaze duration, changes in the frequency of other behaviors may be characteristic of curiosity, as indicated by previous literature. Bubble bursts have been reported as indicative of surprise or play in dolphins and belugas when they are solving a puzzle, witnessing surprising or unexpected events, or playing (Clark, Davies, Madigan, Warner, & Kuczaj, 2013; Delfour & Aulagnier, 1997; Hill et al.,

2011; Pryor, 1990). Open mouth behavior has most commonly been reported as an aggressive behavior, occurring simultaneously with head-to-head orientations, s-postures, jaw claps, abrupt vertical head movements, and chasing behavior (Herzing, 1996; Overstrom, 1983). However, studies of mirror self-recognition also report open mouth behaviors, some of which are classified as contingency checking behavior and appear different to the aggressive open mouth behavior that occurs in social situations (Marten & Psarkos, 1995; Mitchell, 1995; Reiss & Marino, 2001; Sarko, Marino, & Reiss, 2002). It has therefore been suggested that in non-aggressive contexts, open mouth behaviors may indicate interest and excitement (Dudzinski, 1998; Marten & Psarkos, 1995). When killer whales watched a television display as part of an environmental enrichment study the moving display elicited a greater behavioral response, including bubble behaviors, head movements, and open mouths (Hanna et al., 2017).

In order to explore individual differences in curiosity and determine if dolphins perceive certain events to violate expectations in a similar way to other species, a two-part study was conducted. Experiment 1 aimed to explore how dolphins responded to a spontaneously surprising event, which was a jack-in-the-box. Experiment 2 aimed to explore how dolphins reacted when viewing an event that was hypothesized to violate expectations of object continuity, specifically when an object passed through an opaque part of a tube and appeared to transform to another object. Given the ability of dolphins to visually track objects, these animals are likely to find it unusual if one object appears to transform into another object while occluded, and would thus have the longest gaze duration for the most unfamiliar situation with which they are presented. We therefore examined four main hypotheses in the present study: 1) gaze duration was expected to be longer for events and objects that were surprising and violated expectations; 2) in addition to extended looking time, other behaviors were predicted to occur more often in trials with a surprising or expectation-violating event, such as bubble bursts, bubble trails, and open mouth behaviors; 3) there would be individual differences in displays of curiosity behavior; 4) gaze duration was expected to decrease over time because the subjects would habituate to the stimuli.

## Method

### Subjects

The subjects of this study were 15 bottlenose dolphins (6 males, 9 females; 7 adults, 5 juveniles, 3 calves; *Tursiops truncatus*) and 6 rough-toothed dolphins (3 males, 3 females; 4 adults, 2 juveniles; *Steno bredanensis*) housed at Gulf World Marine Park in Panama City Beach, Florida. See Table 1 for a list of subjects' species, sex, and age. Estimated age is used for individuals who were stranding rescues, and age classes were defined as calf (0-2 years), juvenile (3-10 years), and adult (11+ years), per Eskelinen et al. (2015). All 21 subjects completed the first experiment of the study; however, four subjects were excluded from the second experiment, due to two subjects not being present in the habitat and two subjects' failure to observe trials from each of the three conditions. Subjects had daily interactions with training staff, visitors, and environmental enrichment. These interactions took multiple forms, from in-water swims with guests to husbandry sessions, and varied greatly on a day-to-day basis. Social groupings also varied on a daily basis.

Table 1  
*Subjects*

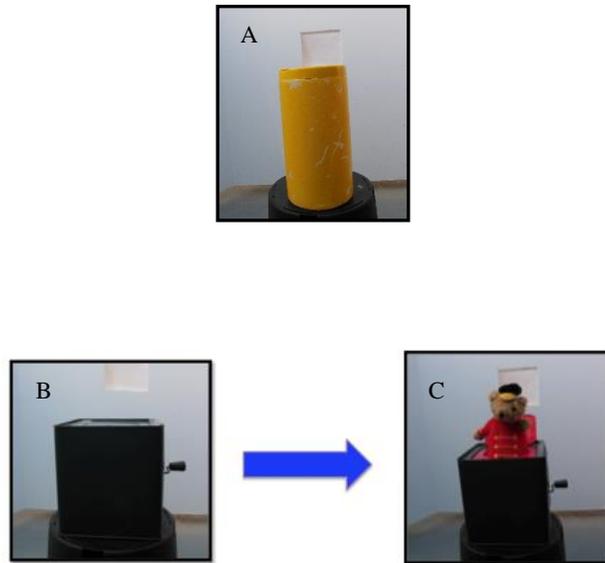
Subject ID	Species	Sex	Age Class
1	Bottlenose	M	Adult
2	Bottlenose	M	Adult
3	Bottlenose	M	Juvenile
4	Bottlenose	M	Juvenile
5	Bottlenose	M	Juvenile
6	Bottlenose	M	Juvenile
7	Bottlenose	F	Adult
8	Bottlenose	F	Adult
9	Bottlenose	F	Adult
10	Bottlenose	F	Adult
11	Bottlenose	F	Adult
12	Bottlenose	F	Juvenile
13	Bottlenose	F	Calf
14	Bottlenose	F	Calf
15*	Bottlenose	F	Calf
16	Rough-toothed	M	Adult
17	Rough-toothed	M	Adult
18	Rough-toothed	F	Adult
19*	Rough-toothed	F	Adult
20*	Rough-toothed	F	Juvenile
21*	Rough-toothed	M	Juvenile

\* Indicates subject not part of Experiment 2

### Procedure for Experiment 1

Data was collected opportunistically when one or more animals were present in front of the underwater window where the study was conducted. Although the dolphins were free to approach or swim away from the window at any time during the session, almost all of the subjects approached the window during each time the apparatus was presented. The experimental apparatus included an opaque screen placed in front of an underwater habitat window. The screen was in place 5 minutes prior to the start of each experimental session to allow for habituation to the screen. In the first experiment, the subjects were shown two different objects: a static cylinder, and a jack-in-the-box. After the habituation period, the first trial began with the static cylinder (Figure 1a), which remained stationary, displayed in front of the opaque screen for 5 minutes, during which time a musical tune was played from the object. The music was intended to attract the subjects' attention to both stimuli, in an attempt to control for differences in water visibility. This allowed subjects to become aware of a new stimulus near the viewing window, even if they were not able to see the stimulus from across the enclosure. After a 5-minute trial was completed, the music stopped and the cylinder was removed. After a period of 1 minute, the jack-in-the-box was placed in front of the screen for a 5-minute trial. The jack-in-the-box was a square box and the surprising event was a small stuffed character popping out of the box when an animal was within 2 meters of the object (Figure 1b and c). The jack-in-the-box played a musical tune that was different from the tune for the control object. After the object emerged, the box was reset after 1-2 seconds. It was then opened again after a random amount of time between 1 and 15 seconds had passed or once a dolphin approached within 2 meters of the jack-in-the-box, whichever happened first. For every trial, a video recording was taken from the perspective of the opaque screen. Every day for 5 consecutive days, each subject was shown a 5-minute trial with the jack-in-

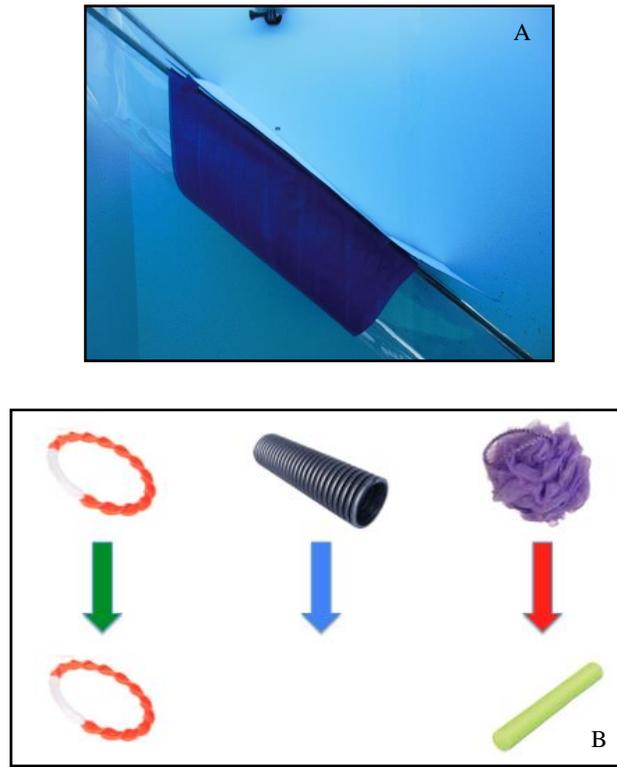
the-box and a 5-minute trial with the cylinder. The presentation of objects was counterbalanced so that on some days, subjects were first presented with the cylinder followed by the jack-in-the-box, and on other days, the presentation order was reversed.



*Figure 1. Pictures of the cylinder control object (Panel A) and the jack-in-the-box without (Panel B) and with (Panel C) a surprise event.*

### **Procedure for Experiment 2**

The second experiment aimed to use the concept of an event violating the subjects' expectations to elicit curiosity. The experimental setup consisted of a clear plastic tube that was 20 cm in diameter and 1 m tall. In the middle of the tube was a 30 cm long opaque section (Figure 2a). This tube was positioned diagonally in front of the screen used in the first phase of the study, and positioned to be in front of an underwater viewing window. Each subject was exposed sequentially to 3 different object transformations (Figure 2b), with 5 trials for each transformation. If individuals saw partial trials, enough trials were conducted such that each individual saw 5 full trials of each transformation. All trials were video recorded for 30 seconds following the object transformation.



**Figure 2. Schematic of the Violation of Expectations (VOE) paradigm (Panel A) including pictures of Object Transformations (Panel B) 1, 2, and 3 (left to right, respectively).**

In Transformation 1, a control object was dropped into the tube when a dolphin approached within 1 meter and remained stationary in front of the underwater viewing window. The object fell through the tube and passed through the opaque section to land at the bottom of the tube. In Transformation 2, the object fell down the tube but did not reappear after the opaque section. In Transformation 3, an object was dropped into the tube and disappeared into the opaque section but another object appeared from the opaque section and fell to the bottom of the tube. Transformation 1 served as a control, where the object remained the same after passing behind the opaque section of the tube. Transformation 2 was hypothesized to be an unexpected event for the subjects because the object did not reappear. Transformation 3 was hypothesized to be even more unexpected to the subjects, as an object appeared to transform to a different object while passing behind the opaque barrier. The objects used for this phase (Figure 2b) were chosen in consultation with animal care staff and were familiar to the subjects; however, objects were counterbalanced in which Transformation Type they were assigned to for each group of individuals typically housed together, to control for any effects due to a specific object in a particular type of transformation.

Gaze duration was defined as the amount of time a dolphin's eye was clearly visible and oriented at the experimental set-up. Every time a subject approached the apparatus, the subject's identification was noted along with gaze duration, and frequency of open mouths ( $>10^\circ$  jaw angle), bubbles trails, and bubble bursts. Reliability between two independent coders was established to be at least .8 (80%) on 20% of the data for each of the behaviors analyzed. Finally, trainers familiar with each subject completed trait ratings on a 7-point Likert scale for 12 items related to curiosity: curious, intelligent, observant, excitable, creative, exploratory, simple, timid, fearful, cautious, bold, and confident.

For Experiment 1, gaze duration was converted to a percentage of time subjects viewed the stimulus out of the time the stimulus was displayed. The frequency of other behaviors were converted to rates by dividing by the time the stimulus was displayed. For both experiments, log transformations were performed for the measures of gaze duration percentage, frequency of open mouths, bubbles trails, and bubble bursts, except gaze duration percentage in Experiment 2, because data for each of these variables had a severely positively skewed distribution. Mixed ANOVAs were performed for sex, species, and Object Type (Experiment 1) or Transformation Type (Experiment 2). In an examination of differences between subjects, mixed ANOVAs were conducted investigating Object or Transformation Type and Subject identity. An additional mixed ANOVA examined age differences across Object or Transformation Type for gaze duration percentage. Finally, to assess the subjects' habituation to the stimuli, repeated measures ANOVAs were conducted comparing gaze duration percentage across the first five trials for each stimulus, in both experiments.

Data for ratings were first analyzed using exploratory factor analysis to determine factor loadings. Scores for each factor were calculated for all subjects and then these scores were correlated with measures of gaze duration percentage.

## Results

### Experiment 1: Object Type, Sex, Species, and Age Class Differences

Several mixed ANOVAs were conducted for Object Type (cylinder vs. jack-in-the-box), sex, and species differences for the dependent variables in Experiment 1. There was a significant effect of Object Type on gaze duration percentage,  $F(1,19) = 12.66, p = 0.002, \eta^2 = 0.40$ , with a significantly greater percentage of time spent viewing the Jack-in-the-box compared to the the cylinder (Figure 3). There was no significant main effect of species on gaze duration percentage,  $F(1,19) = 2.45, p = 0.134, \eta^2 = 0.11$ , nor significant main effect of sex on gaze duration percentage,  $F(1,19) = 1.56, p = 0.226, \eta^2 = 0.08$ ; however, there were descriptive differences in gaze duration percentage between species and sex (Figure 4). An effect of Object Type was found to be approaching significance for the number of open mouths displayed,  $F(1,19) = 3.69, p = 0.070, \eta^2 = 0.16$ , with a greater number of open mouths per trial for the Jack-in-the-box (Figure 5). There was no significant effect of Object Type for number of bubble trails produced,  $F(1,19) = 1.31, p = 0.266, \eta^2 = 0.07$  (Figure 5). There was a significant effect of Object Type on number of bubble bursts produced,  $F(1,19) = 4.36, p = 0.050, \eta^2 = 0.19$  with a significantly greater number of bubble bursts per trial for the Jack-in-the-box compared to the cylinder (Figure 5).

Additionally, a significant interaction between Object Type and age class was found for gaze duration percentage,  $F(2,18) = 5.06, p = 0.018, \eta^2 = 0.36$  (Figure 6). No main effect of age class on gaze duration was found percentage,  $F(2,18) = 0.98, p = 0.394, \eta^2 = 0.10$ . Follow-up analysis revealed that juveniles ( $p = 0.012$ ) and adults ( $p = 0.013$ ) both had a significantly longer gaze duration percentage for the Jack-in-the-box compared to the cylinder, but that no significant difference between Object Type occurred for calves ( $p = 0.463$ ). No other significant interactions nor differences between the sexes, species or age classes were found.

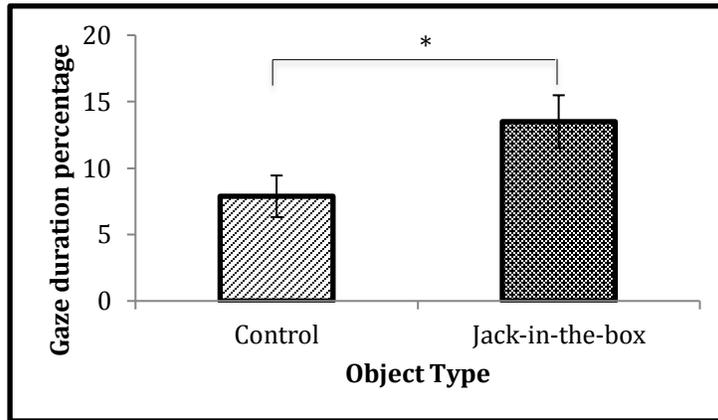


Figure 3. Gaze duration (expressed as a percent of time looking at stimuli) as a function of Object Type (Control, Jack-in-the-box). Error bars are  $\pm$  SEM.  $*p < 0.01$

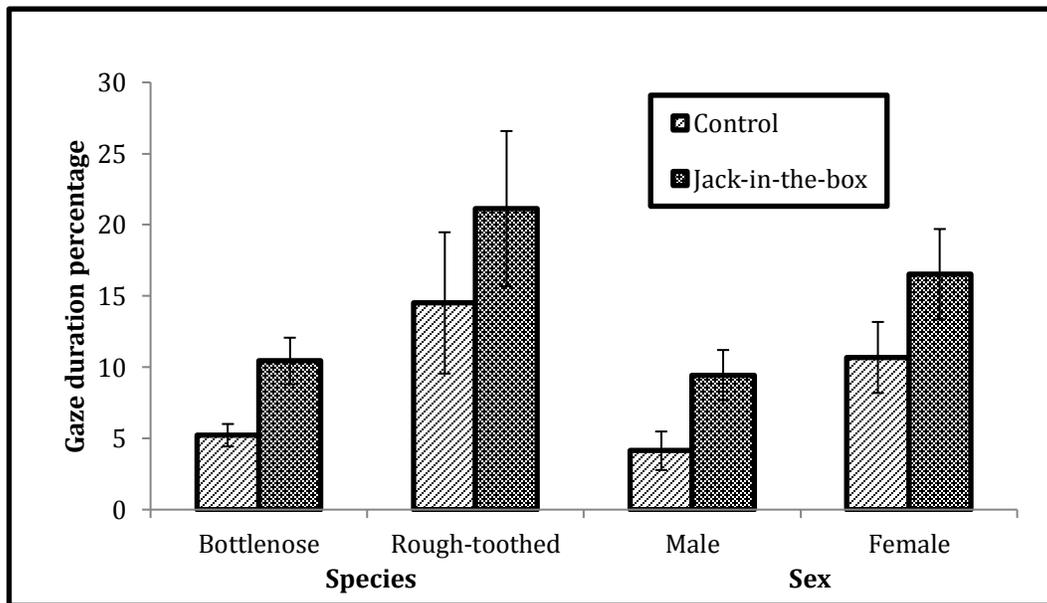


Figure 4. Gaze duration (expressed as a percent of time looking at stimuli) for each Object Type (Control, Jack-in-the-box) as a function of Species (Bottlenose, Rough-toothed) and Sex (Male, Female). Error bars are  $\pm$  SEM.

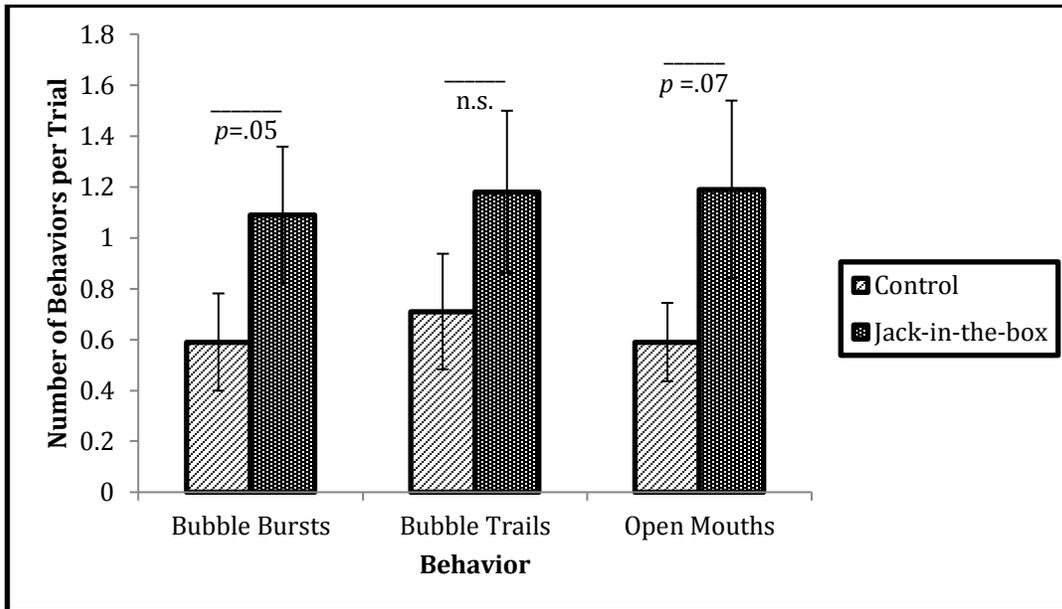


Figure 5. Number of behaviors per trial for each Object Type (Control, Jack-in-the-box) as a function of behavior (Bubble Bursts, Bubble Trails, Open Mouths). Error bars are  $\pm$  SEM.

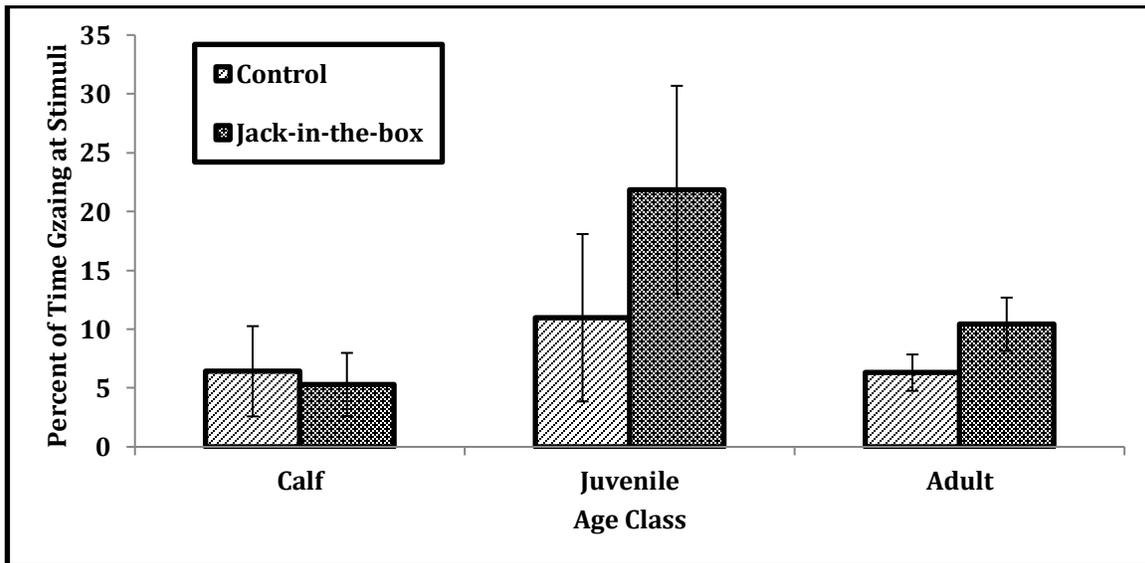


Figure 6. Gaze duration (expressed as a percent of time looking at stimuli) as a function of Age (Calf, Juvenile, Adult). Error bars are  $\pm$  SEM.

### Experiment 1: Exploring Individual Differences

Mixed ANOVAs with Object Type and Subject as independent variables were conducted in order to assess potential individual differences in the dependent variables. A significant interaction was found between Object Type and Subjects,  $F(20,84) = 1.79$ ,  $p = 0.035$ ,  $\eta^2 = 0.30$ . A simple effects analysis found significant

differences between Object Type within Subject 6,  $F(1,84) = 5.85, p = 0.018, \eta^2 = 0.07$ , Subject 10,  $F(1,84) = 4.24, p = 0.043, \eta^2 = 0.05$ , Subject 11,  $F(1,84) = 5.5, p = 0.021, \eta^2 = 0.06$ , Subject 12,  $F(1,84) = 24.05, p < 0.001, \eta^2 = 0.22$ , Subject 17,  $F(1,84) = 4.69, p = 0.033, \eta^2 = 0.05$ , and Subject 20,  $F(1,84) = 7.47, p = 0.008, \eta^2 = 0.08$  (Figure 7). Additionally, there was also a main effect of Subject,  $F(1,20) = 4.88, p < 0.001, \eta^2 = 0.54$ . Because the data violates Levene's, Games-Howell was used as a post hoc test, though none of the comparisons were found to be significant, likely due to the large number of comparisons that were tested.

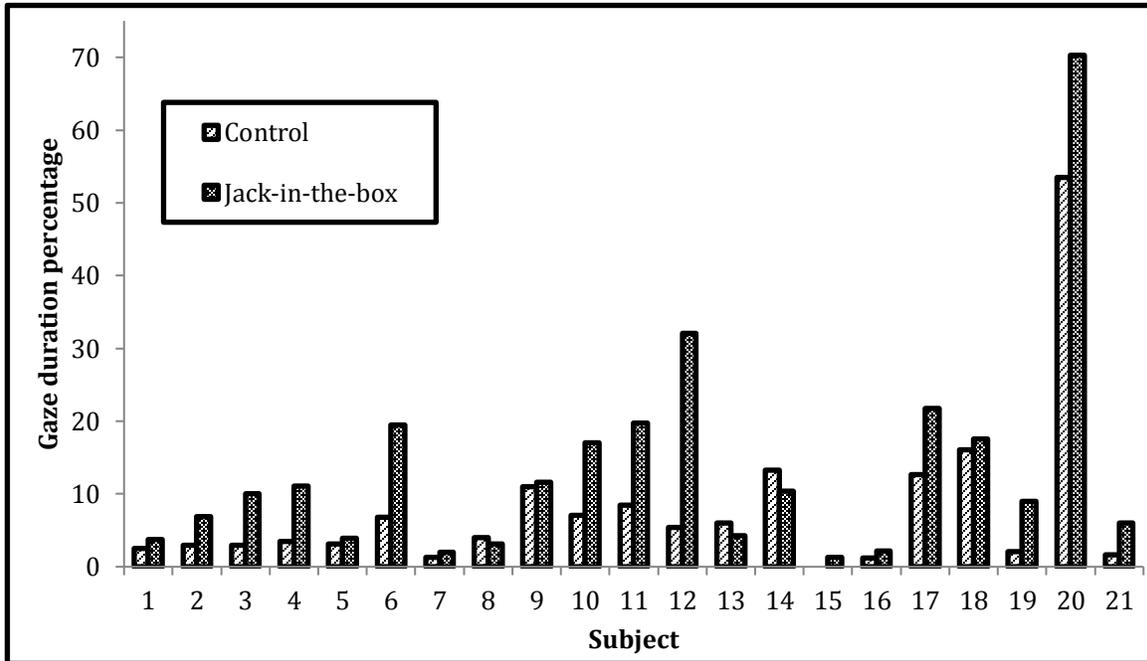


Figure 7. Gaze duration percentage (expressed as a percent of time looking at stimuli) for each Object Type (Control, Jack-in-the-box) as a function of Subject. Subjects 1-6: male bottlenose; Subjects 7-15: female bottlenose; Subjects 16-17, 21: male rough-toothed; Subjects 18-20: female rough-toothed. Subjects in reverse age order within each sex.

No significant main effect of Subject was found for the number of open mouths,  $F(20,84) = 1.26, p = 0.261, \eta^2 = 0.23$ . In contrast, a significant difference in the number of bubble trails between Subjects was found,  $F(1,20) = 6.87, p < 0.001, \eta^2 = 0.62$ ; however, due to such a large number of comparisons, a post hoc Games-Howell test did not reveal any significant differences between any of the Subject comparisons. Similarly, a significant main effect in the number of bubble bursts produced between subjects was found,  $F(1,20) = 3.18, p < 0.001, \eta^2 = 0.43$ ; however, a post hoc Games-Howell test did not reveal any significant differences between any of the Subject comparisons.

## Experiment 2: Transformation Type, Sex, and Species Differences

Mixed ANOVAs were performed to assess Transformation Type, sex, and species differences for Experiment 2. There was an effect approaching significance of Transformation Type on gaze duration,  $F(2,30)$

= 3.10,  $p = 0.060$ ,  $\eta^2 = 0.17$  (Figure 8). A post hoc examination with a Bonferroni correction revealed that gaze duration for Transformation 2 was slightly shorter than gaze duration for Transformation 3 ( $p = 0.061$ ); however, there were no significant differences between Transformation 1 and 3 ( $p = 1.000$ ) or Transformation 1 and 2 ( $p = 0.398$ ).

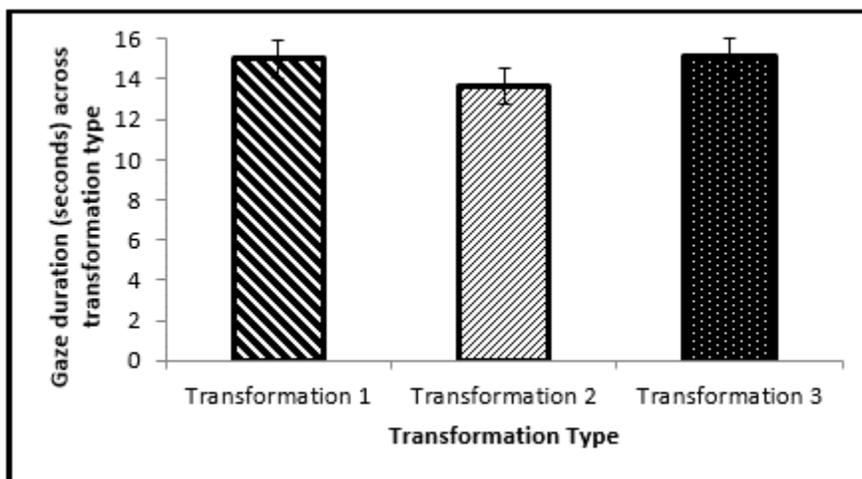


Figure 8. Gaze duration percentage (expressed as a percent of time looking at stimuli) as a function of Transformation Type (1, 2, 3; see Figure 2b).

There was an effect of sex on number of open mouths displayed that approached significance,  $F(1,15) = 4.47$ ,  $p = 0.052$ ,  $\eta^2 = 0.23$ , with females displaying more open mouths per trial compared to males. Additionally, there was a significant effect of species on number of open mouths displayed,  $F(1,15) = 5.04$ ,  $p = 0.040$ ,  $\eta^2 = 0.25$ , with bottlenose dolphins displaying significantly more open mouths per trial compared to rough-toothed dolphins.

There was also a significant effect of species on number of bubble trails produced,  $F(1,15) = 26.01$ ,  $p < 0.001$ ,  $\eta^2 = 0.63$ , with rough-toothed dolphins producing significantly more bubble trails per trial compared to bottlenose dolphins. Finally, there was a significant main effect of sex on number of bubble bursts produced,  $F(1,15) = 12.97$ ,  $p < 0.001$ ,  $\eta^2 = 0.46$ , with females producing significantly more bubble bursts per trial compared to males. No other significant interactions nor differences between the sexes, species, or age classes were found.

## Experiment 2: Exploring Individual Differences

Mixed ANOVAs were conducted to assess individual differences in the dependent variables for Experiment 2. No significant interactions between Transformation Type and Subject were found. A significant main effect of Subject was found for differences in gaze duration,  $F(16,62) = 3.24$ ,  $p < 0.001$ ,  $\eta^2 = 0.46$ . A post hoc Games-Howell test revealed a number of significant differences in gaze duration between several individuals: Subjects 12 and 3 ( $p = 0.001$ ), Subjects 12 and 9 ( $p < 0.001$ ), Subjects 12 and 10 ( $p = 0.009$ ),

Subjects 12 and 5 ( $p = 0.031$ ), Subjects 9 and 4 ( $p = 0.017$ ), and Subjects 9 and 17 ( $p = 0.017$ ). The results between individuals and across Transformation Types are displayed in Figure 9.

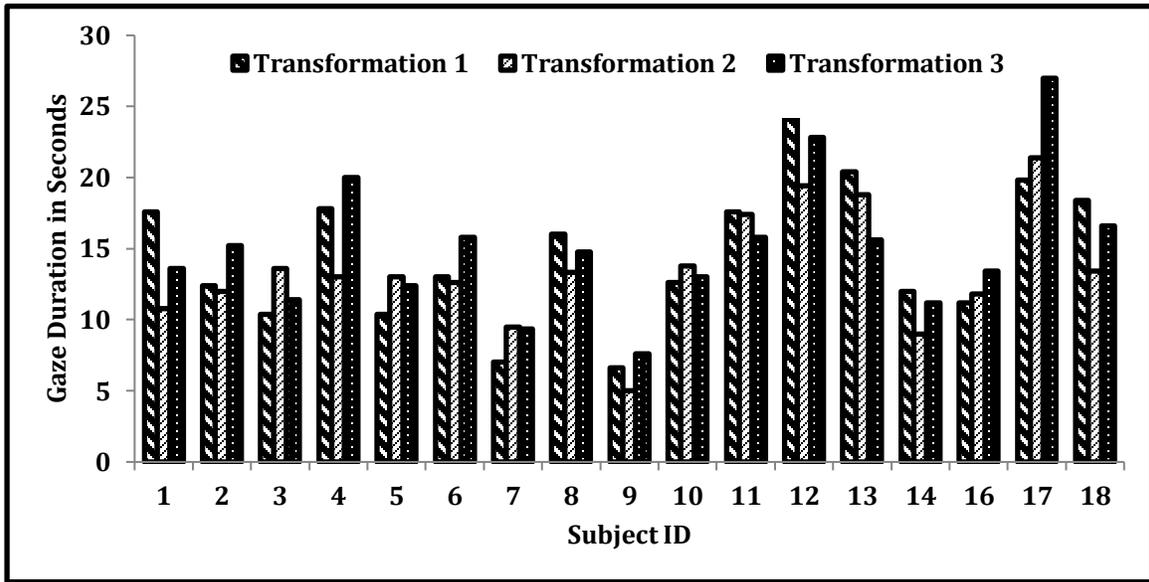


Figure 9. Gaze duration percentage (expressed as a percent of time looking at stimuli) for each Transformation Type (1, 2, 3; see Figure 2b) as a function of Subject. Subjects 1-6: male bottlenose; Subjects 7-14: female bottlenose; Subjects 16-17: male rough-toothed; Subject 18: female rough-toothed. Subjects in reverse age order within each sex.

A significant main effect of Subject on number of open mouth displays was found,  $F(16,62) = 9.99$ ,  $p < 0.001$ ,  $\eta^2 = 0.72$ . A post hoc Games-Howell comparison found differences between a total of 29 different comparisons between individuals. Additionally, a significant main effect of Subject on number of bubble trails produced was found,  $F(16,62) = 3.69$ ,  $p < 0.001$ ,  $\eta^2 = 0.49$ . A post hoc analysis using Games-Howell found that none of the comparisons were significant, likely due to the large number of comparisons that were made. Finally, a significant main effect of Subject on number of bubble bursts was found,  $F(16,62) = 6.27$ ,  $p < 0.001$ ,  $\eta^2 = 0.62$ . A post hoc test using Games-Howell found that Subject 13 was significantly different than seven other subjects.

## Habituation

There were no significant main effects for gaze duration percentage across Trials 1 through 5 for Experiment 1's cylinder,  $F(4,104) = 1.16$ ,  $p = 0.332$  or jack-in-the-box,  $F(4,104) = 1.19$ ,  $p = 0.332$ , nor gaze duration of Experiment 2's Transformation 1,  $F(4, 87) = 1.196$ ,  $p = 0.319$ , Transformation 2,  $F(4, 82) = 0.90$ ,  $p = 0.468$ , or Transformation 3,  $F(4, 84) = 0.30$ ,  $p = 0.877$ .

## Ratings

All trainer ratings on twelve different items were assessed for factors using principle axis factoring. KMO was found to be 0.777 and Bartlett's test of sphericity was found to be significant ( $p < 0.001$ ), indicating adequate sampling and a possible solution. Communalities ranged from 0.371 to 0.730. The model explained a 51.12% of the total variance. The scree plot, as well as theory, indicated that there were two separate factors. The pattern matrix indicated that a factor labeled "Curious" had strong factor loadings of curiosity (0.730), observant (0.695), intelligent (0.729), creative (0.663), excitable (0.640), exploratory (0.607), and a negative loading of simple (-0.625). The second factor labeled "Timid" had factor loadings of timid (0.751), fearful (0.744), and cautious (0.609) and negative factor loadings of confident (-0.707) and bold (-0.729). These values are displayed in Table 2. The factors had a -0.139 correlation with each other. Factor 1 (Curious) had a Cronbach's alpha of 0.849 and factor 2 (Timid) had a Cronbach's alpha of 0.837.

Table 2  
*Factor Loadings for Each Item*

Item	Curious	Timid
Curious	0.730	
Intelligent	0.729	
Observant	0.695	
Excitable	0.640	
Creative	0.633	
Exploratory	0.607	
Simple	-0.625	
Timid		0.751
Fearful		0.744
Cautious		0.609
Bold		-0.729
Confident		-0.707

The scores on both factors were calculated for each subject by summing the average ratings of items on that factor and using the reverse scores of negatively loaded items. The factor scores of each subject were then correlated with the gaze duration percentages of the animals in Experiment 1, using Spearman's rho. The correlation between subjects' gaze duration percentages in the jack-in-the-box trials and their scores on the curious factor was not significant,  $r_s(21) = 0.36$ ,  $p = 0.113$ . The correlation between total gaze duration percentages for both objects of Experiment 1 and the curious factor was approaching significance,  $r_s(21) = 0.43$ ,  $p = 0.055$ . The total gaze duration percentages of Experiment 1 and the factor timid also had a correlation approaching significance,  $r_s(21) = -0.40$ ,  $p = 0.074$ , such that ratings on the factor timid were negatively related to overall gaze duration. Gaze duration percentages for the jack-in-the-box and the factor timid were not significantly correlated,  $r_s(21) = -0.38$ ,  $p = 0.094$ . Finally, the strongest correlation was found between rating scores on the single item "curious" and the total gaze duration percentages for both object of Experiment 1,  $r_s(21) = 0.56$ ,  $p = 0.009$ .

## Discussion

Two main goals of this study were to characterize the curiosity-related behaviors of dolphins and examine individual differences in dolphins' curiosity. Overall, the results indicate that the subjects were more interested in the stimulus with variable movement (jack-in-the-box) compared to a static object (cylinder), and the subjects displayed a wide range of individual differences in their reactions to the stimuli in Experiment 1. Unexpectedly, the object transformations that were hypothesized to violate expectations in Experiment 2 did not capture subjects' interest more than the control condition. Further examination of gaze duration, open mouth, and bubble behaviors as well as differences in species, sex, and trait ratings provided a more complete picture of curiosity in dolphins.

### Experiment 1

The jack-in-the-box stimulus was shown to be significantly more interesting to the subjects compared to the cylinder stimulus, as indicated by differences in gaze duration. Overall, the subjects spent approximately 13.5% of time per trial viewing the jack-in-the-box stimulus compared to 7.9% of time per trial viewing the cylinder stimulus. These results support the idea that devices capable of variable movement are more engaging to dolphins than inanimate objects. This finding is supported by research with other species using visual enrichment, in the form of video stimuli, to provide a variation in the subjects' environment (Ellis & Wells, 2008; Hanna, et al., 2017; Platt & Novak, 1997). Moreover, even though the results of species and sex differences were not statistically different, they did show descriptive differences in their engagement by different visual stimuli. The simple effects analysis revealed that six individuals viewed the jack-in-the-box stimulus for a significantly longer amount of time, though all of the subjects but two calves and one adult had an average longer gaze duration percentage for the jack-in-the-box. A large amount of variation between a single subject's trials likely resulted in a lack of significance both between individuals and also between Object Type for each individual. Individual average jack-in-the-box viewing times ranged from only 1% for Subject 1 to 70% for Subject 20. These results are consistent with other studies that have also found individual differences in dolphins' interest in enrichment and experimental stimuli (Eskelinen et al., 2015; Greene et al., 2011; Hill et al., 2016; Yeater, Hill, Baus, Farnell, & Kuczaj, 2014). While the present study is by no means a comprehensive assessment of environmental enrichment, it does provide information about the preferences of these subjects with regard to the visual stimuli presented. The results may also be representative of the extent of variation that can exist in other populations of dolphins in human care (Eskelinen et al., 2015).

The previous claims that bubble bursts are indicative of surprise, play and excitement in cetaceans (e.g., Clark et al., 2013; Delfour & Aulagnier, 1997; Hill et al., 2011; Pryor, 1990) were substantiated by the results of this study, as 1.8 times more bubble bursts were produced while subjects viewed the jack-in-the-box stimulus compared to when they viewed the cylinder stimulus. In addition, bubble trails were produced 1.7 times more frequently, and 2 times more open mouths occurred, which suggests that they might also be associated with surprise and excitement. Though surprise is not necessarily always positive, complete predictability does not reflect a natural environment, and thus variability can be reinforcing (Sambrook & Buchanan-Smith, 1997). Due to a lack of vocal recording during data collection, it is not known whether or not vocalizations were associated with the observed bubble production, and it is therefore also not known if the subjects vocalized significantly more during the jack-in-the-box condition.

The open mouth behavior displayed by the subjects of this study does not appear to indicate aggression or agitation towards the experimental stimuli. The open mouth behaviors were sometimes related to bubble play that occurred while the subjects were viewing the stimulus, indicating a playful state (Kuczaj & Eskelinen, 2014). No jaw claps, s-postures, or abrupt vertical head movements were directed towards the stimuli or produced in conjunction with the open mouth behaviors, as has previously been recorded in studies of aggression in dolphins (Herzing, 1996; Overstrom, 1983). Furthermore, most instances of aggressive behavior that include open mouth displays are when dolphins are oriented head-to-head with each other or are chasing another animal (Overstrom, 1983); however, in the present study, open mouth behaviors often occurred as the subject was parallel to and pressed up against the viewing window. It has been suggested that the open mouth behavior in the absence of signs of aggression may be signs of excitement and/or play (Dudzinski, 1998; Marten & Psarkos, 1995). After comparison to the contexts of open mouth behavior reported in previous research, the results of the present study suggest the open mouth behavior in the context of unexpected or curiosity-eliciting stimuli may indicate interest and/or surprise, and not aggression. Additionally, no jaw claps were recorded as directed at the experimental apparatus throughout the duration of the experiment, which would have indicated an aggressive and negative reaction to the apparatus. Taken together, the combination of behaviors in this study are similar to the behaviors exhibited by a killer whale while watching a video stimulus (Hanna, et al., 2017).

Species analyses found that the rough-toothed dolphins in this study looked approximately two times longer at the objects presented compared to the bottlenose dolphins. While this could be due to the particular individuals participating in the present study, this difference may represent a species-level difference in curiosity. In a previous study, belugas and bottlenose dolphins were more interested in objects compared to Pacific white-sided dolphins, which the authors suggested may be due to differences in life history pressures and/or the subjects' environment at the time of the study (Guarino et al., 2017). Although neither of these possibilities explains the results of the present study with certainty, it may be that the more pelagic life of the rough-toothed dolphins means that man-made objects are inherently more rare, unfamiliar, and therefore are more interesting to members of that species. Furthermore, all of the rough-toothed dolphins in this study were born in the wild and lived there for some time before stranding and being rescued. Thus, they did not have experience with man-made objects from birth, which some of the bottlenose dolphins did. Alternatively, because the rough-toothed dolphins in the study were stranded, rehabilitated, and housed in the current facility for quite some time, man-made objects were no longer extremely novel. Instead, other factors, such as differences between species in breeding cycles or number of visitor interactions, may have contributed to their longer gaze duration.. Future studies may attempt to account for these other factors by measuring the amount of time each subject is part of interactions with trainers and/or the public on during the course of the study, and by monitoring breeding cycle status.

In the present study, females spent more time looking at the stimuli compared to males. This is partially consistent with previously published literature. Greene et al. (2011) reported that females interacted more with objects compared to the males, while Eskelinen et al. (2015) found that adult males were more likely than adult females to interact with environmental enrichment. The results of Eskelinen et al. (2015) may have been due to many of the females caring for their calves at the time of data collection. During the present study, only one calf was housed with her mother, which meant that other females did not have calves to otherwise occupy their time. Another contributing factor may have been the frequent occurrence of socio-sexual behavior of the males housed together in the present study, which may have diverted their attention from the experimental apparatus. Even though no species or sex differences in gaze duration percentage were found to be statistically significant, there were large descriptive differences, which may be informative for making environmental

enrichment decisions. Of the specific subjects in this study, females and rough-toothed dolphins may benefit more than their counterparts from the use of visual stimuli as enrichment.

Gaze duration percentages between age classes were not found to be significantly different. In addition, each age class, except for the calves, had a longer gaze duration percentage for the jack-in-the-box condition. This result was not unexpected, given the mixed findings from previous studies. Young animals are generally considered to be more curious than older animals, which is consistent with human behavior as well (King, Weiss, & Sisco, 2008; Massen, Antonides, Arnold, Bionda, & Koski, 2013). In contrast, the young subjects of the present study did not display more curiosity compared to older subjects, which may have been due to a number of factors, such as a mother obscuring the calf's view of the stimuli. All other dependent variables were not significantly different between age classes. Future research should aim to compare age classes in more depth, as the subjects in this study were not evenly distributed across age classes.

## **Experiment 2**

The results of Experiment 2 found mostly non-significant differences both between types of object transformations and individuals. Despite most individuals showing an interest in the object transformations with which they were presented, gaze duration for Transformation 3 was longer only compared to Transformation 2, meaning that the subjects did not find an object transforming to another object more interesting than the object remaining the same. This is in contrast to the results of Singer and Henderson (2015), who found that dolphins had a longer gaze duration for expectation-violating condition, in which a bucket seemed to vanish behind a screen. The results of Experiment 2 were also in contrast to the results of many other studies in both human infants and non-human animals exploring the concepts of object permanence, object solidity, and causality (Hauser & Spaulding, 2006; Povinelli & Dunphy-Lelii, 2001; Stahl & Feigenson, 2015). The present study does differ slightly from the above studies in that it was an object transformation instead of a difference in object placement or object appearing to move through a solid material. While the previous studies established that dolphins' expectations can be violated, the present study suggests that a transformation is not as interesting as these other types of expectation-violating events.

Individual differences in gaze duration were also found in Experiment 2, with several different comparisons being statistically significant. Gaze duration ranged from an average of 6 seconds for Subject 9 to 23 seconds for Subject 12. However, there were few significant differences in other behaviors between Transformation Types. Post hoc tests revealed that the only significant difference between individuals was for bubble bursts, in which Subject 13 was found to have significantly more bubble bursts than seven other subjects. Despite the individual differences in bubble burst production, there were no significant differences between conditions, which suggests that bubble bursts are also produced in situations that are not necessarily surprising. The bubble bursts produced during the present study may be attributed to a number of factors, including general interest in the moving experimental stimuli, the sight of familiar objects that are frequently used as secondary reinforcement, a communicative signal for other conspecifics, or possibly a stereotyped response.

In Experiment 2, few species or sex differences were found. Subjects usually viewed the experimental apparatus for several seconds after an object transformation, indicating their general interest in the apparatus, objects, or the movement of the apparatus; however, it does not appear that subjects found Transformation 3 to be an unusual occurrence, nor does it seem that any particular species, sex, or age class found this transformation of particular interest.

Though unexpected, the results of Experiment 2 may indicate that dolphins do not find the apparent transformation of one object to another object to be of particular interest, and/or may not have violated any of the dolphins' expectations. These object transformations may not be an ecologically or evolutionarily important event for dolphins, while others may be more relevant. For example, dolphins may be surprised by the sinking versus floating behavior of ice, with which other non-human animals and human infants would likely be unfamiliar (Kuczaj & Lilley, 2016). Unlike humans, dolphins frequently use echolocation to investigate objects, especially when they cannot visually examine the object. In the present study, the dolphins may have attempted to use echolocation through the underwater viewing windows in order to investigate the disappearance or transformations of objects, but because no acoustic recordings were taken, these attempts cannot be examined. Regardless, it is unlikely that the subjects in this study were able to successfully use echolocation to investigate the objects, as the objects were on the other side of an underwater viewing window with at least several inches of air between the viewing window and the objects used in the experiment. Nevertheless, future research should aim to explore these possible issues by using varied experimental set-ups, by recording vocalizations, using different expectation-violating scenarios, and also using a larger sample size.

### **Trainer Trait Ratings**

Two separate trainer rating factors emerged from the exploratory factor analysis. One contained factor words with a somewhat cognitive-focus, including "curious", while the second factor contained terminology more closely related to the bold-shy continuum. Gaze duration percentages correlated significantly with ratings of the "curious" trait alone. This separation of traits onto separate factors, and the significant correlation of gaze duration percentage only with the curious trait, suggests that the responses to experimental stimuli in the present study reflect curiosity more so than boldness.

Furthermore, these correlations demonstrate that overall interest in stimuli presented to the animals was related to ratings provided by trainers familiar with the subjects. The correlation of the combined gaze duration percentage of subjects in Experiment 1 with the "Curious" factor was approaching significance, as was the negative correlation with the "Timid" factor. Interestingly, ratings of the single item "curious" had a stronger correlation with gaze duration percentage. These correlations indicate that despite a wide range of individual differences in behavior, trainer ratings are related to quantifiable curiosity-related behavior of dolphins. This result supports the use of dolphin personality ratings used in previous studies (Highfill & Kuczaj, 2007; Kuczaj, Highfill, et al., 2012). Furthermore, rating each subject on the term "curious" may be the most efficient way to predict the level of interest a dolphin might have in a visual stimulus, similar to the jack-in-the-box. Though just one curiosity-related behavior, gaze duration percentage, was correlated with the trainer ratings, future research can aim to further explore the connection between trainer ratings for a greater range of personality traits, as well as other behavioral measures. Nevertheless, this study provides evidence that ratings and dolphin behavior are related for measures of curiosity.

Engaging environmental enrichment has been found to increase variation in the behavior of many animals housed at zoological facilities (Swaigood & Shepardson, 2006). Enrichment does not have to be an object that animals can manipulate or eat. Various forms of cognitive enrichment can also play an important role in stimulating the minds of animals (Clark, 2013).

Furthermore, ratings of animal personality have also been used to inform welfare decisions, such as housing and breeding (Tetley & O'Hara, 2012). Personality ratings could also be used to make decisions

regarding environmental enrichment. As seen in the present study, subjects' engagement with the jack-in-the-box stimulus could be dependent on species, sex, age, and differences in personality ratings. Surprise, and the curiosity that follows a surprising event, are both involved in the learning process and are seen in a number of species (Kuczaj, 2017; Piaget, 1952; Stahl et al., 2015). Focusing on these experiences in animals under human care may therefore help enrich their daily lives.

### **Curiosity-Related Behavior in Dolphins**

When presented with a variable and moving stimulus, dolphins are likely to open their mouths, produce bubbles, and continue looking at the surprising stimulus. This pattern of behavior suggests that the dolphins found these stimuli to be engaging, as the subjects often remained very near the underwater viewing window where the experimental apparatus was set up. The dolphins in the present study did not respond to a VOE object transformation with an increase in interest compared to a control condition. This could suggest that dolphins found the movement of all objects, regardless of the transformation, to be of equal interest. Consistent with this, Hill et al. (2016) found that dolphins looked longer at humans who were actively moving, for both familiar and unfamiliar human stimuli. An interesting comparison would be to introduce another condition to Experiment 1 in which a stimulus moved in the same motion as the jack-in-the-box but at a predictable and slow rate. This would reveal whether the general motion of an object would result in the same curiosity-related behaviors or if the spontaneous and unpredictable event of the jack-in-the-box opening is necessary to elicit the reaction found in Experiment 1 of the present study.

Regardless, the subjects in this study were not found to habituate to any of the stimuli over the five separate presentation trials. This indicates that the particular stimuli used in this study were engaging over multiple presentations, a useful quality for any potential environmental enrichment apparatus. Moreover, this lack of habituation is important to the validity of differences (or lack thereof) between the experimental conditions because this means that all trials played an equivalent role in contributing to the averages for each stimulus. Additionally, the lack of habituation to the stimuli provides further evidence that curiosity, rather than neophilia, was being assessed in this study, as subjects were still interested in the stimuli beyond their first exposure.

### **Conclusion**

Differences in species, sex, age, and personality, as rated by trainers, were associated with the extent to which dolphins were interested in visual stimuli. Furthermore, a jack-in-the-box stimulus appeared to elicit increased interest compared to a static object. This study highlights the need to understand and account for individual differences in considerations of environmental enrichment. Though the jack-in-the-box stimulus was of interest to almost all of the study subjects, it was substantially more engaging for some animals compared to others. Contrary to hypotheses, a VOE paradigm did not elicit an increase in subjects' interest more than the control condition. This lack of significant behavioral differences could be due a number of factors and requires exploration in future research. Nevertheless, these results are informative for developing engaging environmental enrichment and determining the behaviors of interest for future research regarding curiosity, surprise, and personality in dolphins.

## References

- Byman, R. (2005). Curiosity and sensation seeking: A conceptual and empirical examination. *Personality and Individual Differences, 38*, 1365–1379. <http://doi.org/10.1016/j.paid.2004.09.004>
- Byrne, R. W. (2013). Animal curiosity. *Current Biology, 23*, R469–R470. <http://doi.org/10.1016/j.cub.2013.02.058>
- Clark, F. E. (2013). Marine mammal cognition and captive care—a proposal for cognitive enrichment in zoos and aquariums. *Journal of Zoo and Aquarium Research, 1*, 1–6.
- Clark, F. E., Davies, S. L., Madigan, A. W., Warner, A. J., & Kuczaj, S. A. (2013). Cognitive enrichment for bottlenose dolphins (*Tursiops truncatus*): Evaluation of a novel underwater maze device. *Zoo Biology, 32*, 608–619. <http://doi.org/10.1002/zoo.21096>
- Dallaire, J. A., Meagher, R. K., & Mason, G. J. (2012). Individual differences in stereotypic behaviour predict individual differences in the nature and degree of enrichment use in caged American mink. *Applied Animal Behaviour Science, 142*, 98–108. <http://doi.org/10.1016/j.applanim.2012.09.012>
- Damerius, L. A., Graber, S. M., Willems, E. P., & van Schaik, C. P. (2017). Curiosity boosts orang-utan problem-solving ability. *Animal Behaviour, 134*, 57–70.
- Delfour, F., & Aulagnier, S. (1997). Bubbleblow in beluga whales (*Delphinapterus leucas*): A play activity? *Behavioural Processes, 40*, 183–186. [http://doi.org/10.1016/S0376-6357\(97\)00782-1](http://doi.org/10.1016/S0376-6357(97)00782-1)
- Dellu, F., Mayo, W., Piazza, P. V. V., Le Moal, M., & Simon, H. (1993). Individual differences in behavioral responses to novelty in rats. Possible relationship with the sensation-seeking trait in man. *Personality and Individual Differences, 15*, 411–418. [http://doi.org/10.1016/0191-8869\(93\)90069-F](http://doi.org/10.1016/0191-8869(93)90069-F)
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals, 24*, 129–142.
- Ellis, S. L., & Wells, D. L. (2008). The influence of visual stimulation on the behaviour of cats housed in a rescue shelter. *Applied Animal Behaviour Science, 113*, 166–174.
- Eskelinen, H. C., Winship, K. A., & Borger-Turner, J. L. (2015). Sex, age, and individual differences in bottlenose dolphins (*Tursiops truncatus*) in response to environmental enrichment. *Animal Behavior and Cognition, 2*, 241–253. <http://doi.org/10.12966/abc.08.04.2015>
- Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology, 75*, 1–20. <http://doi.org/10.1016/j.amjpr.2011.07.011>
- Glickman, S. E., & Sroges, R. W. (1966). Curiosity in zoo animals stable. *Behaviour, 26*, 151–188. <http://doi.org/10.1163/156853966X00074>
- Greene, W., Melillo-Sweeting, K., & Dudzinski, K. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology, 24*, 292–306.
- Guarino, S., Yeater, D., Lacy, S., Dees, T., & Hill, H. M. (2017). Responses to familiar and unfamiliar objects by belugas (*Delphinapterus leucas*), bottlenose dolphins (*Tursiops truncatus*), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). *Animal Cognition, 20*, 823–827. <http://doi.org/10.1007/s10071-017-1103-9>
- Hanna, P., Brown, B., Winship, K., Cameron, D., Hill, H., & Kuczaj, S. (2017). A killer whale's (*Orcinus orca*) response to visual media. *International Journal of Comparative Psychology, 30*.
- Hauser, M., & Spaulding, B. (2006). Wild rhesus monkeys generate causal inferences about possible and impossible physical transformations in the absence of experience. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 7181–7185. <http://doi.org/10.1073/pnas.0601247103>
- Herzing, D. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals, 22*, 61–79.
- Highfill, L. E., & Kuczaj II, S. A. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic Mammals, 33*, 380–389. <http://doi.org/10.1578/AM.33.3.2007.380>
- Hill, H., Kahn, M., Brilliot, L., Roberts, B., Gutierrez, C., & Artz, S. (2011). Beluga (*Delphinapterus leucas*) bubble bursts: Surprise, protection, or play? *International Journal of Comparative Psychology, 24*, 235–243.
- Hill, H., Yeater, D., Gallup, S., Guarino, S., Lacy, S., Dees, T., & Kuczaj, S. (2016). Responses to familiar and unfamiliar humans by belugas (*Delphinapterus leucas*), bottlenose dolphins (*Tursiops truncatus*), & Pacific white-sided dolphins (*Lagenorhynchus obliquidens*): A replication and extension. *International Journal of Comparative Psychology, 29*.

- Hughes, R. N. (1997). Intrinsic exploration in animals: Motives and measurement. *Behavioural Processes*, *41*, 213–226. [http://doi.org/10.1016/S0376-6357\(97\)00055-7](http://doi.org/10.1016/S0376-6357(97)00055-7)
- Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., & Trone, M. (2010). What do dolphins (*Tursiops truncatus*) understand about hidden objects? *Animal Cognition*, *13*, 103–120. <http://doi.org/10.1007/s10071-009-0250-z>
- Johnson, C. M., Sullivan, J., Buck, C. L., Trexel, J., & Scarpuzzi, M. (2014). Visible and invisible displacement with dynamic visual occlusion in bottlenose dolphins (*Tursiops spp.*). *Animal Cognition*, *18*, 179–193. <http://doi.org/10.1007/s10071-014-0788-2>
- King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology*, *122*, 418–427. <http://doi.org/10.1037/a0013125>
- Kuczaj, S. A. (2017). Animal creativity and innovation. In J. Call (Ed.), *APA handbook of comparative psychology*. Washington, DC: APA. <http://doi.org/129>
- Kuczaj, S. A., & Eskelinen, H. C. (2014). Why do dolphins play? *Animal Behavior and Cognition*, *2*, 113. <http://doi.org/10.12966/abc.05.03.2014>
- Kuczaj, S., & Lilley, M. (2016). Out of the mouth of babes: Lessons from research on human infants. *Animal Behavior and Cognition*, *3*, 212–223.
- Kuczaj, S., Highfill, L., & Byerly, H. (2012). The importance of considering context in the assessment of personality characteristics: Evidence from ratings of dolphin personality. *International Journal of Comparative Psychology*, *25*, 309–329.
- Kuczaj, S., Yeater, D., & Highfill, L. (2012). How selective is social learning in dolphins? *International Journal of Comparative Psychology*, *25*, 221–236.
- Kuczaj, S., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology*, *19*, 223–240. Retrieved from <http://escholarship.org/uc/item/4pn1t50s.pdf>
- Kuczaj, S., Lacinak, T., Fad, O., Trone, M., Solangi, M., & Ramos, J. (2002). Keeping environmental enrichment enriching. *International Journal of Comparative Psychology*, *15*.
- Lopes, M. M., Borger-Turner, J. L., Eskelinen, H. C., & Kuczaj, S. A. (2016). The influence of age, sex, and social affiliation on the responses of bottlenose dolphins (*Tursiops truncatus*) to a novel stimulus over time, *3*, 32–45. <http://doi.org/10.12966/abc.02.03.2016>
- Marten, K. & Psarkos, S. (1995). Using self-view television to distinguish between self-examination and social behavior in the bottlenose dolphin (*Tursiops truncatus*). *Consciousness and Cognition*, *4*, 205–224.
- Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*, *75*, 947–958. <http://doi.org/10.1002/ajp.22159>
- Mitchell, R. (1995). Evidence of dolphin self-recognition and the difficulties of interpretation. *Consciousness and Cognition*, *4*, 229–234.
- Overstrom, N. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology*, *2*, 93–103.
- Piaget, J. (1952). *The origins of intelligence in children*. New York: Norton & Company.
- Platt, D. M., & Novak, M. A. (1997). Videostimulation as enrichment for captive rhesus monkeys (*Macaca mulatta*). *Applied Animal Behaviour Science*, *52*, 139–155.
- Povinelli, D. J., & Dunphy-Lelii, S. (2001). Do chimpanzees seek explanations? Preliminary comparative investigations. *Canadian Journal of Experimental Psychology = Revue Canadienne de Psychologie Expérimentale*, *55*, 185–93. <http://doi.org/10.1037/h0087365>
- Pryor, K. (1990). Non-acoustic communication in small cetaceans: Glance, touch, position, gesture, and bubbles. In J. Thomas & R. Kastelein (Eds.), *Sensory ability of cetaceans*. US: Springer. [http://doi.org/10.1007/978-1-4899-0858-2\\_37](http://doi.org/10.1007/978-1-4899-0858-2_37)
- Reiss, D. & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *PNAS*, *98*, 5937–5942.
- Sambrook, T. & Buchanan-Smith, H. (1997). Control and complexity in novel object enrichment. *Animal Welfare*, *6*, 207–216.

- Santos, L. R., Barnes, J. L., & Mahajan, N. (2005). Expectations about numerical events in four lemur species (*Eulemur fulvus*, *Eulemur mongoz*, *Lemur catta* and *Varecia rubra*). *Animal Cognition*, 8, 253–262. <http://doi.org/10.1007/s10071-005-0252-4>
- Sarko, D., Marino, L., & Reiss, D. (2002). A bottlenose dolphin's (*Tursiops truncatus*) responses to its mirror image: Further analysis. *International Journal of Comparative Psychology*, 15, 69–76.
- Singer, R., & Henderson, E. (2015). Object permanence in marine mammals using the violation of expectation procedure. *Behavioural Processes*, 112, 108–113. <http://doi.org/10.1016/j.beproc.2014.08.025>
- Stahl, A. E., & Feigenson, L. (2015). Observing the unexpected enhances infants' learning and exploration. *Science*, 348, 91–94. <http://doi.org/10.1126/science.aaa3799>
- Swaisgood, R. & Shepardson, D. (2006). Environmental enrichment as a strategy for mitigating stereotypes in zoo animals: A literature review and meta-analysis. In G. Mason & J. Rushed (Eds.), *Stereotypic animal behaviour: Fundamentals and applications to welfare 2<sup>nd</sup> ed.* (pp. 256–285). Wallingford, UK: CAB International.
- Tetley, C., & O'Hara, S. (2012). Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo animals. *Animal Welfare*, 21, 463–476.
- Thieltges, H., Lemasson, A., Kuczaj, S., Böye, M., & Blois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Animal Cognition*, 14, 303–308. <http://doi.org/10.1007/s10071-010-0354-5>
- Wilson, D., Clark, A., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442–446.
- Yeater, D., Hill, H., Baus, N., Farnell, H., & Kuczaj, S. (2014). Visual laterality in belugas (*Delphinapterus leucas*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) when viewing familiar and unfamiliar humans. *Animal Cognition*, 17, 1245–1259.

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