Animal Behavior and Cognition
ABC 2016, 3(1):32-45
DOI: 10.12966/abc.02.03.2016

The Influence of Age, Sex, and Social Affiliation on the Responses of Bottlenose Dolphins (*Tursiops truncatus*) to a Novel Stimulus Over Time

Melissa M. Lopes[1, 2, *], **Jill L. Borger-Turner**[1, 2, 3], **Holli C. Eskelinen**[1, 3], **& Stan A. Kuczaj II**[4]

[1]Dolphins Plus Oceanside
[2]Rosenstiel School of Marine and Atmospheric Science, University of Miami
[3]Dolphins Plus Bayside
[4]University of Southern Mississippi

*Corresponding author (Email: melissa@dolphinsplus.com)

Citation – Lopes, M., Borger-Turner, J. L., Eskelinen, H. C., & Kuczaj, S. A. II. (2016). The influence of age, sex, and social affiliation on the responses of bottlenose dolphins (*Tursiops truncatus*) to a novel stimulus over time. *Animal Behavior and Cognition, 3*(1), 32–45. doi: 10.12966/abc.02.03.2016

Abstract - Responses to novelty may differ among individuals as a function of age, sex, and/or the presence of offspring, and understanding how marine mammals respond to novel stimuli is critical to management. In this study, 20 captive Atlantic bottlenose dolphins (*Tursiops truncatus*) were exposed to a novel object, consisting of PVC pipes and either a non-reflective or reflective surface. Their responses, broadly defined as either non-social or social, non-aggressive or aggressive interactions with the stimulus, were recorded across 10 exposure trials and compared among age classes and between males and females. Adult females exhibited the highest frequency of interactions, and those with dependent calves participated in more social interactions. Both adults and calves displayed a significantly greater frequency of interactions and aggression when exposed to the reflective versus non-reflective surface, indicating that the characteristics of the stimulus influenced the response. Although the number of interactions did not change across repeated exposures, there were significantly more aggressive interactions during later exposures, suggesting sensitization to the stimulus. There was no evidence of habituation over time for any of the subjects. Thus, when managing marine mammal exposure to anthropogenic stimuli, it is important to consider the demographics of the population, as well as the characteristics of the stimulus that may contribute to habituation, sensitization, and/or tolerance.

Keywords – Bottlenose dolphin, *Tursiops truncatus*. Behavioral response, Novel stimulus, Enrichment, Neophobia, Sensitization

The novelty of an object is characterized by the difference between past and present experiences with the object, such that the greater the difference, the more novel the object (Corey, 1978). When animals are exposed to novel objects, responses are typically characterized as, but not limited to, exploration, orientation, avoidance, and/or aggression (e.g., Bowles & Anderson, 2012; Fu, Zhao, Qi, Guo, Wei, & Li, 2013; Greenberg & Mettke-Hofmann, 2001). Given the potential consequences and rewards associated with each type of response, understanding how a cognitively advanced species, such as dolphins, respond to novel stimuli may assist with predictions regarding their ability to adapt to an ever-changing environment and various anthropogenic stimuli. Neophilia, described as the approach or exploration of a novel object to acquire information (see Fu et al., 2013), can lead to the acquisition of important resources and increase an animal's fitness (Kuczaj, Lacinak, Fad, Trone, Solangi, & Ramos, 2002; Kuczaj, Winship, & Eskelinen, 2015). Conversely, neophobia is defined as the avoidance of, or apprehension towards, a novel object in an effort to circumvent potential dangers (see Fu et al., 2013). Both neophilia and neophobia have been noted and described in many species of animals, including rats (*Rattus norvegicus*) (e.g., Barnett, 2007; Mitchell, 1976), garden warblers (*Sylvia borin*; Mettke-Hofmann, Rowe, Hayden, & Canoine, 2006), pumpkinseed sunfish (*Lepomis gibbosus*; Wilson, Coleman, Clark, & Biederman, 1993), non-human primates (e.g., Visalberghi & Addessi, 2003; Yamamoto & Lopes, 2000), and marine mammals (Bowles & Anderson, 2012) following exposure to novel objects, food items, and environments.

The characteristics of a novel object (e.g., shape, size, complexity, and location) have been shown to influence the responses of animals (e.g., Greenberg & Mettke-Hofmann, 2001; Heinrich, Marzluff, & Adams, 1995; Mettke-Hofmann et al., 2006). In a study conducted by Mettke-Hofmann et al. (2006), more complex objects elicited a stronger behavioral response from garden warblers (*Sylvia borin*) than simpler objects (e.g., longer durations of exploration, stronger avoidance responses). They theorized that complex objects might be associated with a greater level of uncertainty. Therefore, while the object could provide more information and thus, more potential benefits, it could also harbor dangerous materials and greater potential risks.

Novel stimuli may also promote diverse reactions among individuals, including differences associated with sex, age, social hierarchy, and personality/temperament. Although literature describing animal personalities and novelty is scarce, some studies have noted individual differences across various species including birds, mammals, and reptiles (e.g., Carere & van Oers, 2004; Kuczaj, Highfill, & Byerly, 2012; Lopez, Hawlena, Polo, Amo, & Martín, 2005). Age is also suggested to play a role in the likelihood of an animal approaching novel objects and engaging in exploratory or play behaviors, with mixed reported outcomes described in controlled exposure studies (e.g., Fu et al., 2013; Kuczaj et al., 2002, 2006, 2012; Reader & Laland, 2001; Yamamoto & Lopes, 2004). As with age, there are no consistent effects associated with one sex versus the other in response to novel stimuli. For example, in a study of capuchin monkeys (*Cebus libidinosus*), males exhibited a greater frequency of interaction with novel stimuli when compared to females (Visalberghi & Addessi, 2003), while another study reported a stronger neophilic response from female common marmosets (*Callithrix jacchus*) (Yamamoto & Lopes, 2004).

The presence of conspecifics and social relationships can also have an impact on an animal's behavior towards novel stimuli. Among Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), subordinate individuals exhibited greater neophilic responses towards novel objects compared to more dominant individuals (Fu et al., 2013). This has also been observed in other species, including birds: common starlings (*Sturnus vulgaris*; Boogert, Reader, & Laland, 2006), western jackdaws (*Corvus monedula*; Katzir, 1982), barnacle geese (*Branta leucopsis*; Stahl, Tolsma, Loonen, & Drent, 2001), and capuchin monkeys (e.g., di Bitetti & Janson, 2001), in which subordinate individuals tended to approach novel stimuli first and were then commonly displaced by more dominant individuals. Exploration and other neophilic responses towards novel stimuli have also been positively correlated with the presence of a conspecific and are most pronounced among parents and their offspring (Stöwe et al., 2006). For example, in a study of titi monkeys (*Callicebus moloch*), there was no significant difference in the latencies to approach novel objects between parents and their adult and subadult offspring (Mayeaux & Mason, 1998).

The amount of time an individual is exposed to a novel stimulus may also have an effect on the type of response it elicits. When regularly presented over time, the novelty associated with an object decreases and may become subject to habituation, defined as a decrease in response or exploratory behavior over time (for review, see Leussis & Bolivar, 2006). However, repeated exposure to a novel stimulus may also lead to sensitization, defined as an increase or amplification in response over time (Groves & Thompson, 1970). For example, in a study of 10 animal species, all study subjects were more likely to interact with and orient towards novel objects presented for shorter and more variable time intervals (Kuczaj et al., 2002), and rodents, similarly, exhibited a decrease in the duration and intensity of exploratory behaviors when repeatedly exposed to a novel environment (Leussis & Bolivar, 2006).

Studies to date have shown that dolphins possess the ability to discriminate between familiar and unfamiliar stimuli. Thieltges, Lemasson, Kuczaj, Boye, and Blois-Heulin (2011) discovered that the duration of bottlenose dolphin (*Tursiops truncatus*) gazes upon an object were longer when it was unfamiliar. Bowles and Anderson (2012) exposed several different marine mammal species, including dolphins, to novel objects and found that all species appeared fearful of the objects and predominantly avoided or displayed aggressive behaviors towards the novel stimuli. Additionally, Delfour and Herzing (2013) exposed a group of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) to an underwater mirror and observed exploration of the novel object by mother/calf pairs, as well as aggressive displays from a male dolphin. In the wild, dolphins are likely exposed to both familiar and novel stimuli regularly, and their ability to adapt is critical to both individual and species survival (e.g., Reiss, McCowan, & Marino, 1997). By studying the effects of novel stimuli on the individual and group behavior of bottlenose dolphins (*Tursiops truncatus*), it may be possible to predict the impacts of anthropogenic stimuli on wild populations. In this study, captive bottlenose dolphins were exposed to a novel object stimulus with two states (reflective and non-reflective), and their responses were recorded in an experimental setting to determine the influence of age, sex, social affiliation, and repeated exposures.

Method

Setting and Subjects

This study was conducted at Dolphins Plus Oceanside, Island Dolphin Care, and Dolphins Plus Bayside, three zoological facilities in Key Largo, Florida. Dolphins Plus Oceanside and Island Dolphin Care are located on a public access canal, open to the Atlantic Ocean at both ends, dividing the area into two, main enclosures (i.e., “North Lagoon” and “South Lagoon”). Each enclosure encompasses 836 m^2 of submerged limestone and algal habitat, with a mean depth of 4 m (± 1.2 m). Dolphins Plus Bayside consists of a single 1000 m^2 lagoon on Florida Bay, with a mean depth of 6 m (± 1.2 m). All three enclosures are semi-open systems, which allow for the partial, daily exchange of natural seawater associated with the ~ 1 m tidal range in the area. All of the dolphins at each facility were utilized as study subjects ($n = 20$), including males and females of varying age classes, defined as: calf (dependent and nursing), juvenile (pseudo-independent and not nursing), subadults (independent but not sexually mature), and adults (sexually mature) (Table 1).

Equipment

A unique apparatus, composed of PVC (1 m^2) and either a reflective surface of acrylic mirror or a non-reflective surface (i.e., black cloth covering acrylic), was utilized as a novel stimulus to elicit responses from the study population (Figure 1). The two surface types were used to assess the potential impacts of variation in the characteristics of a novel object on dolphin responses. Visual data were recorded, for both the reflective and non-reflective trials, using three, underwater digital cameras and one above water camera. A GoPro HERO was mounted to the top left corner of the PVC frame and a Canon Powershot D10 was inserted in the middle of the mirror. Additionally, a Canon G9 Power Shot 12.1 mega-pixel was placed approximately 1 m below the water surface in the enclosure, using a monopod, to collect peripheral data, and a Canon G12 Power Shot 12.1 mega-pixel was stationed topside to collect above water data.

Table 1

Dolphin Study Subjects: Location, Name, Sex, and Age Class

Facility	**Animal Name**	**Sex**	**Age Class**
Dolphins Plus Bayside	Alfonz	M	Adult
	Kimbit	M	Adult
	Samantha (Sam)	F	Adult
	Leo	M	Subadult
	Elvis	M	Subadult
	Nica	F	Subadult
	Julie	F	Juvenile
	Isaac	M	Calf
Dolphins Plus Oceanside/Island Dolphin Care North	Sarah	F	Adult
	Dinghy	F	Adult
	Jessica	F	Adult
	Fiji	M	Subadult
	Zoe	F	Calf
	Baby Bit (BB)	F	Calf
	Grace	F	Calf
Dolphins Plus Oceanside/Island Dolphin Care South	Bob	M	Adult
	Bella	F	Adult
	Squirt	F	Adult
	Lotus	F	Juvenile
	Tashi	M	Calf

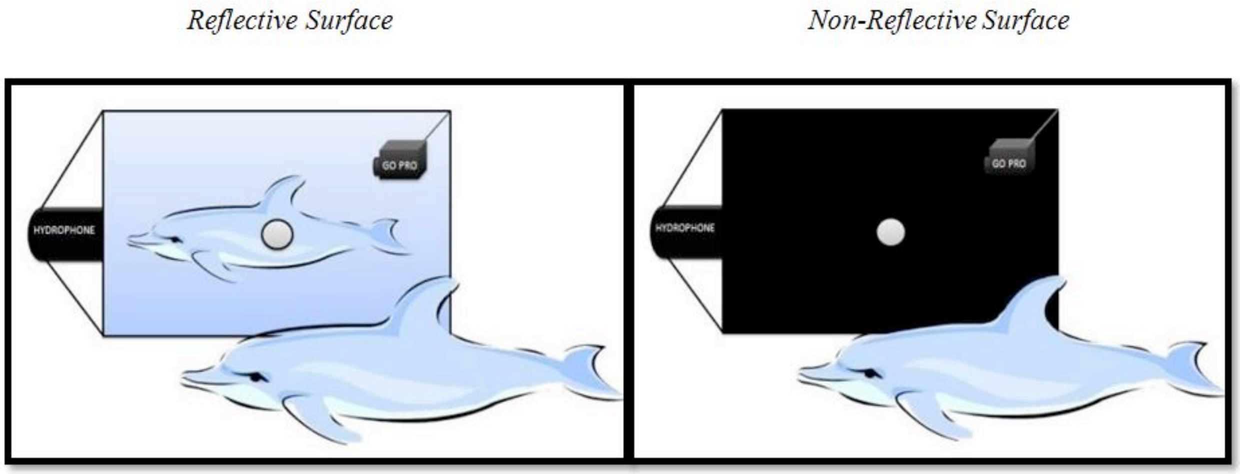

Figure 1. A diagram of the experimental apparatus (i.e., the “stimulus”) utilized to assess dolphin behavioral responses.

Sampling Protocol

Experimental trials. All dolphins within each enclosure were exposed to the stimulus 10 times (5 reflective, 5 non-reflective) for 20 min over the course of two weeks in September 2012. All experimental trials were conducted on days in which high tide occurred in the morning, between the hours of 7:00 a.m. and 12:00 p.m., and during favorable weather and water conditions (i.e., sunny and good visibility). The animals in this study were completely naïve to the apparatus prior to the initial exposure. Reflective and non-reflective trials were randomly assigned with constraints to allow for comparisons in novel responses between the non-reflective and reflective surfaces. There were a total of 30 trials and 600 min of data. All behaviors exhibited in response to the stimulus were recorded and catalogued using an all-occurrence sampling methodology (Altmann, 1974). When comparing novel vs. non-novel responses to the stimulus, only the first trial in each enclosure was considered novel or "early exposure," and only the last trial was considered non-novel or "late exposure" (see Kuczaj et al., 2002).

Data collection. In all of the experimental trials (n = 30), the behavioral responses of the dolphins were recorded using video cameras and *in situ* above water observations. Prior to the deployment of the stimulus, group behavior within the enclosure was recorded for 10 min with a video camera and then assessed using a general, qualitative behavioral ethogram to note any anomalous behaviors. This preliminary assessment was completed before each trial and provided a baseline of behavioral state pre-trial and was used qualitatively in fine scale analyses. Following the 10 min pre-trial data collection, the apparatus was completely submerged below the surface of the water and secured to the seawall for a total of 20 min. During the trial, all of the dolphins within the enclosure had access to all sides of the apparatus with the exception of the back, which was against the seawall. When the 20-min trial was complete, the stimulus was removed completely from the water and moved out of sight. All trials were conducted under the same experimental conditions (e.g., time of day, position of apparatus, method of deployment, and weather).

Interactions with the apparatus were defined as an individual(s) stopping or moving within 1 m of the apparatus, and the interaction was terminated when the individual(s) moved out of the 1 m range. The total number of interactions per individual was recorded, as well as whether or not interactions occurred involving a single animal (i.e., "non-social") or with two or more dolphins engaging in an interaction simultaneously (i.e., "social"). A behavioral ethogram was utilized to quantify the frequency of occurrence per 20 min trial of specific positional configurations and relative proximities to the apparatus during social interactions, in order to identify which individuals were most likely to have initiated the interaction (i.e., those anterior to other group members and closest to the apparatus upon approach). Lastly, the frequency of aggressive behaviors per individual was also recorded and characterized as interactions involving any of the following behaviors, singularly or in combination, directed towards the apparatus: tail thump, tail slap, tail swat, jaw clap, threat, hunch, head shake, and/or open mouth.

Analyses. The mean frequency of interactions (social and non-social) and aggression exhibited by all subjects, as well as their position relative to the apparatus and other dolphins during social interactions, were compared across each series of 10 trials. These behaviors were compared among individuals using a one-way ANOVA and post hoc tests (Bonferroni). Standardized comparisons were made between males and females using a t-test. Lastly, comparisons of frequency of interactions and aggression were made between reflective versus non-reflective trials, as well as between early vs. late exposure to the stimulus, using independent t-tests.

Results

Response to Stimulus – Number of Interactions (Total and Social)

The total mean (± SD) number of interactions with the apparatus per trial, including all trials ($N = 30$) and subjects ($N = 20$), was 23 (± 16), and of those, the mean (± SD) number of social interactions was 15 (± 14). There was a significant difference in the mean number of interactions recorded among subjects (One-way ANOVA: $F(19, 180) = 17.19$, $p < 0.05$). Bella interacted with the stimulus significantly more frequently than all other subjects, and Squirt and Sam exhibited significantly more social interactions, along with their dependent calves, Tashi and Isaac (One-way ANOVA: $F(19, 180) = 28.63$, $p < 0.05$). Elvis interacted with the stimulus significantly less often and less often in social groups than all other subjects (Figure 2).

There were no significant differences in the total number of interactions per trial between males and females, but there were differences in the number of social interactions between sexes. Females displayed a greater frequency of social interactions compared to males (Independent t-test: $t(18) = 6.24$, $p < 0.05$), and mothers with dependent calves (i.e., Ding, Jessica, Sarah, Sam, Squirt) exhibited significantly more social interactions with the stimulus than all other individuals (one-way ANOVA: $F(19, 180) = 28.63$, $p < 0.05$). There was no difference in the number of social interactions between mothers and their dependent calves (Figure 2). Among females, those that were not mothers or dependent calves exhibited significant differences in the frequency of social interactions with the stimulus during the study; however, these differences varied individually and were not consistent across a specific age class. Among males, calves that were paired with their mothers interacted significantly more frequently with the apparatus and significantly more often in social groups than subadult and adult males who were not pair bonded with any other individuals (one-way ANOVA: $F(2, 77) = 147.83$, $p < 0.05$). Among age classes (males and females combined), subadults were recorded interacting with the apparatus significantly less frequently than calves, juveniles, and adults (one-way ANOVA: $F(3, 136) = 17.10$, $p < 0.05$) (Figure 2). During social interactions, adults initiated significantly more interactions than calves and subadults, and juveniles initiated significantly more than subadults (one-way ANOVA: $F(3, 196) = 13.94$, $p < 0.05$) (Figure 3).

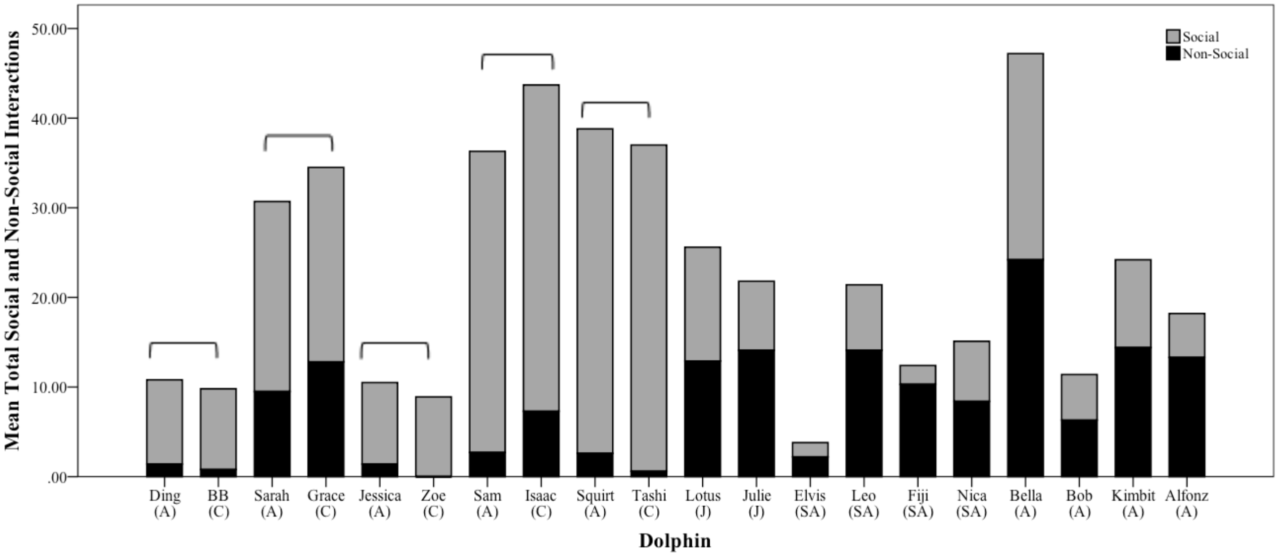

Figure 2. Mean number of social and non-social interactions with the apparatus per trial ($n = 10$) exhibited by each subject ($N = 30$), identified as individuals and their age class: calf (C), juvenile (J), subadult (SA), and adult (A). Brackets delineate mother-calf pairs.

Figure 3. Mean (±1SE) proportion of the total number of social interactions initiated by each age class (calf, juvenile, subadult, and adult).

Response to Stimulus – Aggression

The mean (± SD) number of aggressive interactions with the apparatus per trial ($n = 10$), including all trials and subjects, was 1.0 (± 2). There was a significant difference in the mean number of aggressive interactions recorded among subjects (one-way ANOVA: $F(19, 180) = 5.27$, $p < 0.05$) (Figure 4). Squirt, Grace, Kimbit, and Julie exhibited the greatest frequency of aggressive interactions towards the stimulus, compared to BB, Jessica, Zoe, Lotus, and Elvis, who were not recorded exhibiting any aggressive behaviors in response to the stimulus during the study period (one-way ANOVA: $F(19, 180) = 5.27$, $p < 0.05$).

Females were significantly more aggressive in the presence of the apparatus than males (Independent t-test: $t(18) = 2.10$, $p < 0.05$) (Figure 5), and there were significant intrasexual differences. Among females, Squirt, Julie, Sarah, and Grace responded to the stimulus with the greatest mean number of aggressive displays during interactions across all trials (one-way ANOVA: $F(11, 108) = 5.29$, $p < 0.05$) (Figure 4). All mothers and their dependent calves, excluding Squirt and Tashi, responded similarly to the stimulus in terms of the frequency of aggressive behaviors. Squirt was aggressive significantly more often during an interaction with the apparatus than Tashi (one-way ANOVA: $F(19, 180) = 5.27$, $p < 0.05$). Among males, Kimbit and Alfonz exhibited significantly more aggressive interactions with the apparatus per trial than Fiji, Bob, Leo, and Elvis (one-way ANOVA: $F(6, 23) = 5.72$, $p < 0.05$) (Figure 4). Among age classes (males and females combined), adults exhibited the greatest frequency of aggressive interactions and differed significantly from calves and subadults (one-way ANOVA: $F(3, 36) = 5.60$, $p < 0.05$) (Figure 4).

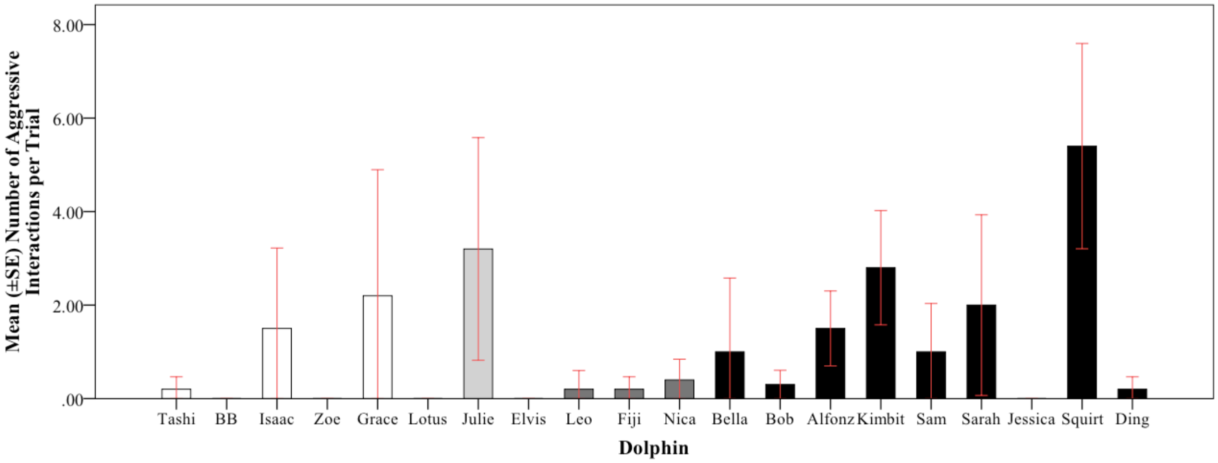

Figure 4. Mean (± 1 SE) number of aggressive interactions with the apparatus per trial (n = 10) exhibited by each subject (N = 30) and age class (calf = white, juvenile = light grey, subadults = dark grey, and adults = black).

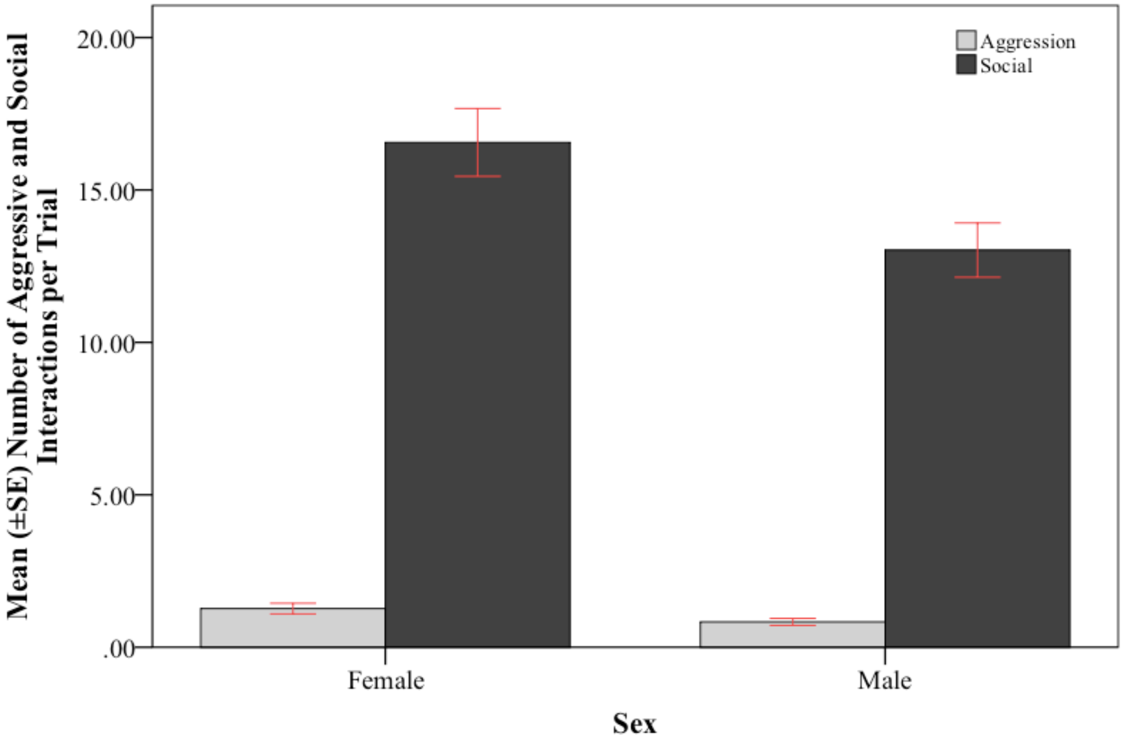

Figure 5. Mean (± 1 SE) number of aggressive and social interactions with the apparatus per trial (n = 10) exhibited by male and female dolphins.

Reflective versus Non-Reflective Trials

There were significantly more interactions, both total and social, per trial for all subjects combined when exposed to the reflective surface versus the non-reflective surface (independent t-test: $t(198) = 1.38$, $p < 0.05$) (Figure 6 and 7). Additionally, the number of social interactions was significantly higher during the reflective trials for mother-dependent calf pairs Sam-Isaac and Squirt-Tashi but significantly lower for Sarah-Grace (Figure 7). Among age classes, adults and calves interacted with the stimulus significantly more frequently than any other age class when exposed to the reflective surface of the stimulus (independent t-test: $t(88) = 1.19$, $p < 0.05$). Females interacted with the stimulus significantly more often when exposed to the reflective surface (independent t-test: $t(118) = 0.79$, $p < 0.05$), while there was no significant difference in the total number of interactions between surfaces identified for males. The opposite effect was observed for social interactions. Males interacted with the reflective surface significantly more often in groups (independent t-test: $t(78) = 1.20$, $p < 0.05$).

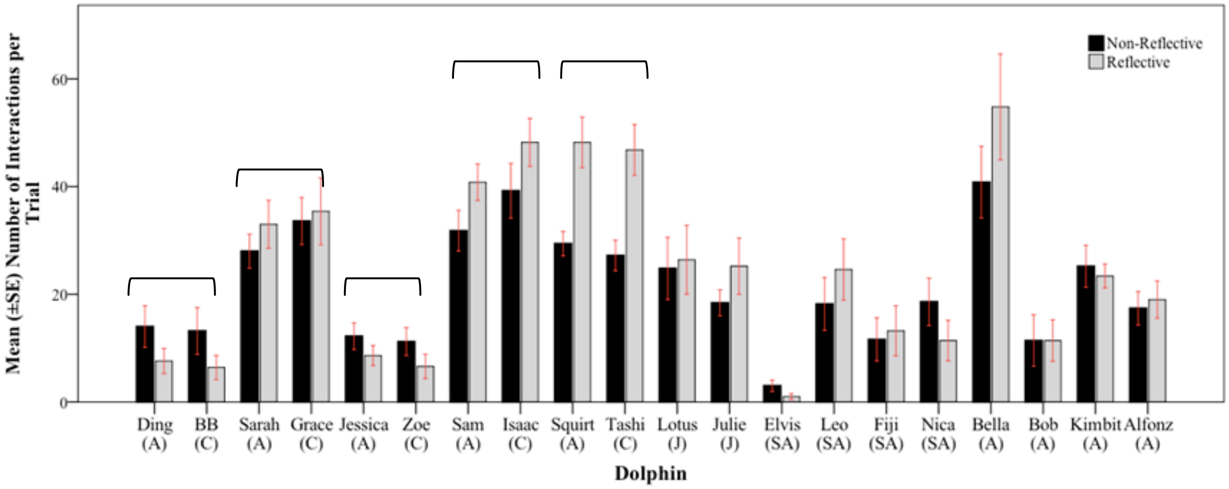

Figure 6. Mean (± 1 SE) number of interactions with the reflective and non-reflective surfaces of the apparatus for each subject ($N = 30$), identified as individuals and their age class: calf (C), juvenile (J), subadult (SA), and adult (A). Brackets delineate mother-calf pairs.

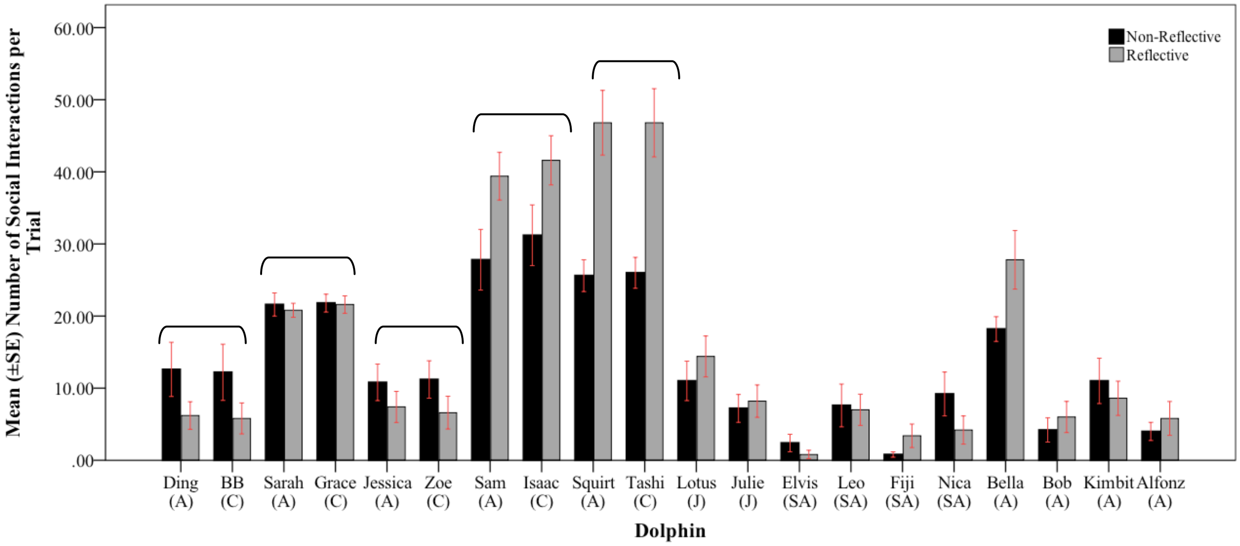

Figure 7. Mean (± 1 SE) number of social interactions exhibited in response to the reflective and non-reflective surfaces of the apparatus for each subject ($N = 30$), identified as individuals and their age class: calf (C), juvenile (J), subadult (SA), and adult (A). Brackets delineate mother-calf pairs.

There were significantly more aggressive interactions for all subjects combined, males and females, when exposed to the reflective surface versus the non-reflective surface (independent t-test: $t(198) = 1.37$, $p < 0.05$). Sarah, Grace, Sam, Isaac, and Squirt displayed a greater mean frequency of aggression when presented with the reflective surface versus the non-reflective surface, while Bella was significantly less aggressive with the reflective surface when compared to the non-reflective surface (Figure 8). Between males and females, males exhibited no difference in the frequency of aggression between the reflective and non-reflective surfaces, while females exhibited a significantly greater frequency of aggression during reflective trials (independent t-test: $t(118) = 1.21$, $p < 0.05$). Among age classes, calves, juveniles, and adults all displayed a greater frequency of aggressive interactions when exposed to the reflective versus non-reflective surface of the stimulus (independent t-test: $t(158) = 1.28$, $p < 0.05$). Mother-calf pairs did not differ significantly in their responses to each surface, except for Squirt who exhibited significantly more aggression during both reflective and non-reflective trials than her calf Tashi (independent t-test: $t(18) = 4.70$, $p < 0.05$).

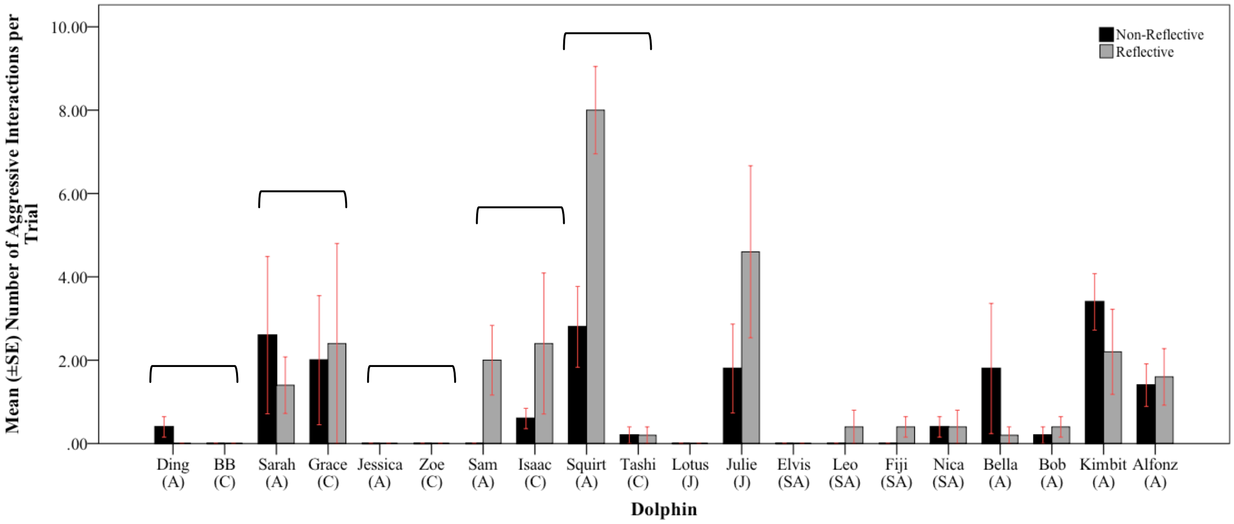

Figure 8. Mean (± 1 SE) number of aggressive interactions exhibited by each subject ($N = 30$) in response to the reflective and non-reflective surfaces of the apparatus, identified as individuals and their age class: calf (C), juvenile (J), subadult (SA), and adult (A). Brackets delineate mother-calf pairs.

Early versus Late Exposure

For all 20 subjects, there was no significant difference in the mean number of interactions between early and late exposure to the stimulus. However, there were significantly more aggressive interactions and significantly less social interactions during late exposures versus early exposures (independent t-test: $t(789) = 2.72$, $p < 0.05$); (independent t-test: $t(789) = 2.29$, $p < 0.05$).

Discussion

The results of this study suggest that there may be a variety of influences (i.e., sex, age, individual differences, and social affiliation) on the responses of bottlenose dolphins when exposed to a novel object. More than half of the total interactions with the apparatus involved two or more dolphins, which was expected, given that bottlenose dolphins are considered a highly social species with dynamic hierarchies (Connor, Wells, Mann, & Read, 2000). Though interactions conducted in groups could represent typical patterns of group formation outside of experimental trials, the individuals engaging with the apparatus together often exhibited similar response topographies (e.g., swimming in the same direction, orienting with the same eye). Though bonded individuals often exhibit synchronicity (see Bauer & Harley, 2001; Fellner, Bauer, & Harley, 2006), mimetic behavior can occur via social learning when interest in an object is stimulated by observing others interacting with the same object (Kuczaj & Yeater, 2006). For example, monkeys are more likely to eat novel foods when other group members are eating the same foods (e.g., Visalberghi & Addessi, 2003; Visalberghi & Fragaszy, 1995). Many of the group interactions with the apparatus in this study involved adult females with their offspring. In many cases, if the mother was not with her calf during an interaction, the calf was accompanied by an alloparent, classified as another adult female, and calves rarely interacted with the stimulus alone. Since half of the female study subjects were either a mother or a dependent calf, this could explain the high frequency of noted social interactions. A similar behavioral response was observed with titi monkeys, such that the latency associated with their approach towards a novel object did not differ between adults and their offspring (Mayeaux & Mason, 1998).

Previous studies have noted a decline in neophilia in animals with age, such that the oldest individuals exhibit the weakest response towards novel objects (e.g., Huffman, 1996; Kummer & Goodall, 1985; Mayeaux & Mason, 1998). In some cases, this is correlated with social status, such that older, more dominant individuals may try to influence younger, subordinate individuals to approach novel objects and thus, incur the potential costs (Boogert et al., 2006). However, in this study, adults were observed approaching and initiating interactions significantly more than calves and subadults. Three of the four subadults in this study were males who were not notably pair bonded with any other individuals within their enclosures, and they exhibited the weakest neophilic response towards the novel object. Therefore, social affiliations with adults, particularly bonds between mothers and calves, may be a strong influencing factor in regards to a dolphin's decision to approach or avoid a novel object. Approaching a novel object with other conspecifics increases group vigilance and protection and thus, may decrease the likelihood of a potential threat (Neumann & Orams, 2006).

Unfamiliar stimuli have the potential to elicit aggressive behavior if perceived as a threat, and complex novel objects may elicit stronger neophilia or neophobia than more simple objects (Mettke-Hofmann et al., 2005). Aggression towards the apparatus was more frequently observed among females when compared to males and more frequently when the reflective surface was presented. Previous studies have indicated that male bottlenose dolphins exhibit significantly more aggression than females; however, this most commonly occurs within the context of herding females or in aggressive interactions with other alliances (Connor et al., 2000; Scott et al., 2005). In another exposure study, a single male dolphin and two adult females exhibited aggressive behaviors (e.g., charging) when exposed to unfamiliar objects, supporting the theory that certain stimuli have the potential to be aversive, and females may display more aggressive behaviors in specific scenarios (Bowles & Anderson, 2012; Delfour & Herzing, 2013). This aggressive response may become further pronounced in the presence of their calves, as has been observed in wild bottlenose dolphin populations (Mann & Smuts, 1999). Additionally, more complex objects, including size, color, and/or shape, can elicit stronger behavioral responses, such as longer durations of exploration, since these objects carry more information (Kuczaj et al., 2002; Mettke-Hofmann et al., 2005). Given the increase in aggression among females associated with the reflective surface, this characteristic was likely perceived as more aversive than the non-reflective surface. Among males, they interacted significantly more frequently in groups than alone when presented with the reflective surface, potentially capturing a greater level of apprehension.

Habituation to a stimulus is evidenced by a decrease in behavioral responsiveness over time if the stimulus is neither perceived as favorable or aversive (see Bejder, Samuels, Whitehead, Finn, & Allen, 2009). There was no significant decrease in interactions over time, and, as such, habituation did not likely occur within the timeframe of this study (i.e., ten, 20-min trials over the course of two weeks). Though it is possible that habituation occurred immediately during the first trial (see Kuczaj et al., 2002; Thieltges et al., 2011), greater frequencies of aggression noted in later trials suggests that the subjects became sensitized to the apparatus over time. Sensitization, an increase in behavioral responsiveness over time due to the averseness or reinforcing properties of a stimulus (see Bejder et al., 2009), has been observed in animals exposed to anthropogenic stimuli (e.g., Alves, Andriolo, Orams, & Azevedo, 2012; Bejder et al., 2009). Bowles and Anderson (2012) found that several species of marine mammals appeared fearful of novel objects and predominantly avoided or displayed aggressive behaviors towards the objects at some point during trials. The dolphins in this study appeared to become sensitized to the apparatus over time, resulting in increased aggression, due to the potentially aversive properties of the apparatus. However, it is also possible that as the novel object became more familiar, the animals' apprehension decreased over time, thus allowing them to engage in more agonistic interactions. Longer exposures and trials may have eventually resulted in habituation.

Complex novel objects can be utilized in an experimental setting to assess individual and group responses while simultaneously providing a form of cognitive enrichment (Clark, Davies, Madigan, Warner, & Kuczaj, 2013). Our results indicate that the decision of an individual to interact with a novel object is driven by multiple influences simultaneously, including but not limited to social affiliation, age, and sex, thus demonstrating the behavioral plasticity of bottlenose dolphins, considered a cognitively advanced species (e.g., Marino, 2002). The ability to discriminate between novel and familiar objects is fundamental to animals' reactions towards stimuli, and these decisions have significant adaptive influences, including identifying potential opportunities and benefits (e.g., prey, foraging strategies, and habitats) and avoiding potential dangers (e.g., nets) (Greenberg & Mettke-Hofmann, 2001). The ability to explore and be flexible allows animals, such as the bottlenose dolphin, to be well equipped for change, ultimately resulting in increased fitness and both individual and species survival (Sabbatini, Stammati, Tavares, & Visalberghi, 2007). This work contributes to our understanding of how bottlenose dolphins respond to novel stimuli and may be utilized to manage and mitigate anthropogenic influences in the wild.

Acknowledgements

The authors gratefully acknowledge the Research and Animal Care staffs at Dolphins Plus Oceanside, Dolphins Plus Bayside, and Island Dolphin Care for their assistance and support of this project. We would also like to thank the anonymous reviewers for their thoughtful comments and suggestions for strengthening the manuscript.

References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3), 227–266.

Alves, L. C. P. S., Andriolo, A., Orams, M. B., & Azevedo, A. F. (2012). The growth of 'botos feeding tourism,' a new tourism industry based on the boto (Amazon river dolphin) *Inia geoffrensis* in the Amazonas State, Brazil. *Sitientibus Serie Ciencias Biologicas*, *11*, 8–15.

Barnett, S. A. (2007). *The rat: A study in behaviour*. Transaction Publishers. Chicago: Aldine.

Bauer, G. B., & Harley, H. E. (2001). The mimetic dolphin. *Behavioral and Brain Sciences*, *24*, 326–327.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, *395*, 177–185.

Boogert, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, *72*, 1229–1239.

Bowles, A. E., & Anderson, R. C. (2012). Behavioral responses and habituation of pinnipeds and small cetaceans to novel objects and simulated fishing gear with and without a pinger. *Aquatic Mammals*, *38*, 161.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (*Parus major*): Body temperature and breath rate in response to handling stress. *Physiology & Behavior*, *82*, 905–912.

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.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In: J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91 – 126). Chicago: The University Press.

Corey, D. T. (1978). The determinants of exploration and neophobia. *Neuroscience & Biobehavioral Reviews*, *2*, 235–253.

Delfour, F., & Herzing, D. (2013). Underwater mirror exposure to free-ranging naïve Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. *International Journal of Comparative Psychology, 26*, 158-165.

Di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *62*, 47–56.

Fellner, W., Bauer, G. B., & Harley, H. E. (2006). Cognitive implications of synchrony in dolphins: A review. *Aquatic Mammals*, *32*, 511–516.

Fu, W., Zhao, D., Qi, X., Guo, S., Wei, W. E. I., & Li, B. (2013). Free-ranging Sichuan snub-nosed monkeys, *Rhinopithecus roxellana*: Neophobia, neophilia, or both. *Current Zoology*, *59*, 311–316.

Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. *Current Ornithology, 16*, 119–178.

Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, *77*, 429–450.

Heinrich, B., Marzluff, J., & Adams, W. (1995). Fear and food recognition in naive common ravens. *The Auk*, *112*, 499–503.

Huffman, M. A. (1996). Acquisition of innovative cultural behaviors in nonhuman primates: A case study of stone handling, a socially transmitted behavior in Japanese macaques. In: C. M. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 267–289). London: Academic Press

Katzir, G. (1982). Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula*, 1. Response to novel space. *Behaviour*, *81*, 231–263.

Kuczaj, S. A., Higfill, 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. A., Lacinak, T., Fad, O., Trone, M., Solangi, M., & Ramos, J. (2002). Keeping environmental enrichment enriching. *International Journal of Comparative Psychology*, *15*, 127–137.

Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. A. (2006). The role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphins calves. *International Journal of Comparative Psychology, 19,* 223–240.

Kuczaj, S. A., II, Winship, K. A., & Eskelinen, H. C. (2015). Can bottlenose dolphins (*Tursiops truncatus*) cooperate when solving a novel task? *Animal Cognition, 18*, 543–550. doi: 10.1007/s10071-014-0822-4

Kuczaj, S. A., & Yeater, D. B. (2006). Dolphin imitation: Who, what, when, and why? *Aquatic Mammals*, *32*, 413–422.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*, 203–214.

Leussis, M. P., & Bolivar, V. J. (2006). Habituation in rodents: A review of behavior, neurobiology, and genetics. *Neuroscience & Biobehavioral Reviews*, *30*, 1045–1064.

Lopez, P., Hawlena, D., Polo, V., Amo, L., & Martín, J. (2005). Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour*, *69*, 1–9.

Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain Behavior and Evolution*, *59*, 21–32.

Mayeaux, D. J., & Mason, W. A. (1998). Development of responsiveness to novel objects in the titi monkey, *Callicebus moloch*. *Primates*, *39*, 419–431.

Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*, 529–566.

Mettke-Hofmann, C., Rowe, K. C., Hayden, T. J., & Canoine, V. (2006). Effects of experience and object complexity on exploration in garden warblers (*Sylvia borin*). *Journal of Zoology*, *268*, 405–413.

Mitchell, D. (1976). Experiments on neophobia in wild and laboratory rats: A reevaluation. *Journal of Comparative and Physiological Psychology*, *90*, 190–197.

Neumann, D. R., & Orams, M. B. (2006). Impacts of ecotourism on short-beaked common dolphins (*Delphinus delphis*) in Mercury Bay, New Zealand. *Aquatic Mammals*, *32*, 1–9.

Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, *22*, 787–805.

Reiss, D., McCowan, B., & Marino, L. (1997). Communicative and other cognitive characteristics of bottlenose dolphins. *Trends in Cognitive Sciences, 1*, 140–145.

Sabbatini, G., Stammati, M., Tavares, M. C. H., & Visalberghi, E. (2007). Response toward novel stimuli in a group of tufted capuchins (*Cebus libidinosus*) in Brasilia National Park, Brazil. *American Journal of Primatology*, *69*, 457–470.

Scott, E. M., Mann, J., Watson-Capps, J.J., Sargeant, B.L., & Connor, R.C. (2005) Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behavior. *Behaviour*, *142*, 21–44.

Stahl, J., Tolsma, P. H., Loonen, M. J., & Drent, R. H. (2001). Subordinates explore but dominants profit: Resource competition in high Arctic barnacle goose flocks. *Animal Behaviour*, *61*, 257–264.

Stöwe, M., Bugnyar, T., Loretto, M. C., Schloegl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes*, *73*, 68–75.

Thieltges, H., Lemasson, A., Kuczaj, S. A., Boye, M., & Blois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Animal Cognition*, *14*, 303–308.

Visalberghi, E., & Addessi, E. (2003). Food for thought: Social learning about food in capuchin monkeys. In: D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 187–212). Cambridge, UK: Cambridge University Press.

Visalberghi, E., & Fragaszy, D. (1995). The behaviour of capuchin monkeys, *Cebus paella*, with novel food: The role of social context. *Animal Behaviour*, *49*, 1089–1095.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*, 250–260.

Yamamoto, M. E., & de Araújo Lopes, F. (2004). Effect of removal from the family group on feeding behavior by captive *Callithrix jacchus*. *International Journal of Primatology*, *25*, 489–500.