Age-related Aspects of Mirror-use by Bottlenose Dolphins (Tursiops truncatus)

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Age-related Aspects of Mirror-use by Bottlenose Dolphins (*Tursiops truncatus*)

by

Rachel Morrison

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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ABSTRACT

Age-related Aspects of Mirror-use by Bottlenose Dolphins (Tursiops truncatus)

by

Rachel Morrison

Advisor: Dr. Diana Reiss

Bottlenose dolphins are neuroanatomically different and evolutionarily divergent from primates yet they exhibit mirror self-recognition (MSR), a rare cognitive ability in non-human animals. This research investigated the developmental and age-related aspects of MSR in this species. During a longitudinal study, a social group of bottlenose dolphins at the National Aquarium, Baltimore, MD were exposed to a mirror and their behavioral responses were recorded to: 1) further confirm the presence of MSR in this species, 2) determine the age of emergence of MSR and 3) draw comparisons with data documenting the emergence of this ability in humans and great ape species. Based on previous research it was predicted that the dolphins in this study would demonstrate the ability for MSR. It was also predicted that due to the precocious motor and social development of bottlenose dolphin calves, MSR would emerge in dolphins at an age comparable to humans and chimpanzees. Results confirmed the presence of this ability in dolphins as all three of the dolphins tested passed the mark test. Results also supported the prediction that MSR emerges in dolphins at an age comparable to humans and chimpanzees and notably self-directed behavior was observed at an even earlier age in dolphins. Bayley, the youngest dolphin was observed demonstrating self-directed behavior in front of the mirror on her fourth day of mirror exposure, at ~5 ½ months of age. For all of the dolphins, almost no social behavior was observed on the first day of mirror exposure, which is not surprising because these dolphins were not naïve to reflective surfaces. Findings from this study also contradict previous
research with chimpanzees that has shown older individuals lose interest in mirrors. Nani, the oldest dolphin (~37 years), had less access to the mirror and yet spent more time at the mirror than Bayley. This research provides important insights into how highly encephalized species, like humans, apes, and dolphins compare developmentally with respect to the age of emergence and developmental stages of MSR. Documentation of such socio-cognitive development is critical to our understanding of the evolution of intelligence in the animal world. Other contributions of this research include: 1) a more in depth analysis of the emergence of mirror-directed behavior and a reevaluation of the categorization of these behaviors, taking into account context and 2) a discussion of the importance of focusing and relying on compelling self-directed behavior exhibited at the mirror as an indicator of MSR and less reliance on only considering positive mark test results as sufficient evidence for this ability.
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Introduction

History of mirror self-recognition (MSR) studies with humans and other animals

Mirror self-recognition (MSR), the ability to recognize oneself in a mirror, was once thought to be restricted to humans. MSR is a visual index of self-awareness, which Gallup (1982) defined as “the ability to become the object of your own attention (p. 243)”. To date, MSR has also been documented in great apes (Gallup, 1970, 1982; Miles, 1994; Patterson & Cohn, 1994; Posada & Colell, 2007; Povinelli, Rulf, Landau, & Bierschwale, 1993; Suarez & Gallup, 1981; Westergaard & Hyatt, 1994), bottlenose dolphins (*Tursiops truncatus*) (Reiss & Marino, 2001), Asian elephants (*Elephas maximus*) (Plotnik, de Waal, & Reiss, 2006), and possibly magpies (*Pica pica*) (Prior, Schwarz, & Güntürkün, 2008). A more recent study with jackdaws has suggested that there may have been methodological issues with the mark-tests conducted with magpies (Soler, Pérez-Contreras, & Peralta-Sánchez, 2014). Results of many studies conducted with monkeys have shown that they do not possess MSR. However, a recent study reported that rhesus monkeys, in atypical conditions in which they had undergone surgical head implants for electrophysiological recordings, exhibited self-directed behavior at a mirror to the external head implants and other areas of their bodies in post surgical observations (Rajala, Reininger, Lancaster, & Populin, 2010). Whether the rhesus monkeys’ behavior constitutes evidence for MSR remains unclear. The presence of MSR in humans, great apes, dolphins, elephants, and magpies has been suggested as evidence for cognitive convergence in these evolutionarily divergent species (Plotnik et al., 2006; Reiss & Marino, 2001).

Other species with varying amounts of prior mirror experience do not seem to demonstrate MSR, but are capable of “mirror-guided behavior,” the use of mirrors as tools to explore their environment and may include using a mirror to locate hidden conspecifics, food, or
other objects. Mirror-guided behavior has been reported in pygmy marmosets (Eglash & Snowdon, 1983), African grey parrots (Pepperberg, Garcia, Jackson & Marconi, 1995), pigs (Broom, Sena & Moyham, 2009), and New Caledonian crows (Medina, Taylor, Hunt, & Gray, 2011). This type of behavior supports the idea that some animals are capable of learning that a relationship exists between the information they see in the mirror and the features in their surrounding environment (Broom et al., 2009). These comparative studies are important for understanding how different species perceive and process mirror information (Pepperberg et al., 1995).

In his seminal study, Gallup (1970) was the first to show evidence that a non-human primate species, the chimpanzee (Pan troglodytes) was capable of MSR. Gallup (1970) observed the behavior of 4 preadolescent mirror naïve chimpanzees throughout isolated mirror exposure over a 10-day period (80 hrs total). His results demonstrated a decrease in social behaviors at the mirror within the first 2 days and an increase in self-directed behaviors. Gallup (1970) considered the chimpanzee’s performance of self-directed behavior at the mirror evidence of MSR, but in order to measure MSR more objectively and to confirm the presence of this ability further, Gallup (1970) developed the mark test. In this test, a visible mark was placed on an area of the body that can only be seen in the mirror. Once the chimpanzees started showing self-directed behavior, they were anesthetized and marked above their brow ridge and on the top edge of the opposite ear with a red odorless dye (Gallup, 1970). Prior to reinstating the mirror, 30-minute observations were conducted noting the number of mark-directed responses in the absence of a mirror. These observations were then compared to the number of mark-directed responses once the mirror was returned. Gallup’s (1970) results concluded that there were more mark-directed responses when the mirror was present and the duration of time spent at the mirror.
increased after being marked. Traditionally, in non-human MSR studies, the animal is thought to pass the mark test if there is more mark-directed behavior following re-introduction of the mirror and an increase in self-directed behaviors with extended mirror exposure (Bard, Todd, Bernier, Love, & Leavens, 2006; Gallup, 1970; Povinelli et al., 1993).

In order to better describe the behavioral responses of children to a mirror, the first preliminary study of the development of MSR in children was conducted by Dixon (1957) with a small group of children (twins & individuals) aged 4 to 16 months. Amsterdam (1972) conducted a more controlled 2-year developmental study of MSR with a larger sample (88 children) of children between the ages of 3 to 24 months. Independently from Gallup (1970), Amsterdam (1972) developed the “rouge” test for use with human infants. In this early study, children’s responses to the mirror were observed over three short (~5-minute) trials following their mothers marking the side of their nose with rouge and being placed in a playpen in front of the mirror. To ensure that the children were motivated to look in the mirror, the mothers were asked to scaffold their child by verbally prompting them saying “see, see, see (Amsterdam, 1972, p. 299)” while pointing to the child’s reflection in the mirror and also asking the child who is in the mirror. Unlike in Gallup’s (1970) study, the children were not observed over several days prior to being marked (Amsterdam, 1972). Although the criteria for passing the mark test in children varies to some extent between studies, children have been reported to pass the mark test if they either touch the mark, touch their face near the mark, say their name when asked who is in the mirror, or point to themselves (Anderson, 1984; Bard, et al., 2006). According to Anderson (1984), in order for an individual to pass the mark test they must first have a mental representation of what their image looks like so that they can make comparisons with the marked image in the mirror.

Exhibiting self-directed behavior and passing the mark test has been considered to be the
standard procedure for determining whether or not individuals can recognize themselves in a mirror, regardless of the species being tested. Notably, not all children and apes tested pass the mark test even though they show self-directed behavior at the mirror, which Gallup (1970) considered to be behavioral evidence for MSR. Only 13 (54%) of the 18-24 month old children that participated in Amsterdam’s (1972) original study passed the mark test, in an early comparative study of the development of MSR in a chimpanzee and an orangutan, neither individual passed the mark test (Robert, 1986), and in a later developmental study only 75% of the 12 chimpanzees aged 8-15 years old passed (de Veer, Gallup, Theall, van den Bos, & Povinelli, 2002). As a result, it has been suggested that researchers need to be cautious about assuming that mark test results are the essential ingredient of MSR (Povinelli et al., 1993).

Although they may have used different terms, these previous studies established that during mirror exposure, humans and great apes that have demonstrated the ability for MSR show three distinct stages of behavior: 1) exploratory/social behavior, which is characterized by examining the mirror, attempting to look over, under, or behind it and the exhibition of social responses as if reacting to a conspecific, 2) contingency-testing (CT), the performance of repetitive behaviors in front of the mirror that appear to represent the individual perceiving and understanding a corresponding relationship between its own behavior and what it observes in the mirror (learning the rules of the mirror use), and 3) self-directed behavior, which involves the individual examining parts of their body that can only be seen using the mirror or monitoring their own behavior at the mirror (Amsterdam, 1972; Dixon, 1957; Gallup, 1970). When testing individuals that are completely mirror naïve (they have no prior experience with reflective surfaces), the behaviors exhibited have generally followed the aforementioned sequence. The transition between stages is not always clear and the length of time that each individual exhibits
behaviors from each stage can vary depending on their age or developmental level. For example, some studies have shown that social behaviors and even contingency-testing behaviors may last for only a short period of time. Some of the chimpanzees in Povinelli et al.’s (1993) study began producing self-exploratory behaviors within 10-20 minutes of mirror exposure. However, during testing, individuals that have prior experience with reflective surfaces may not exhibit social behaviors, but instead will exhibit repetitive or even self-directed behaviors (Reiss & Marino, 2001). Species that fail the mark test and do not demonstrate MSR do not advance to stage three (self-directed behavior).

Comparative developmental studies of MSR in children and chimpanzees have demonstrated that social and exploratory behavior is typically first demonstrated by children between 4-6 months of age (Amsterdam, 1972; Dixon, 1957), peaking between 6-8 months of age (Amsterdam, 1972) and in chimpanzees social behavior is first seen between 7-9 months of age (Robert, 1986). The next stage of behavior (contingency-testing) is typically seen in children by the end of the first year (Amsterdam, 1972); however, Dixon (1957) reports starting to see repetitive behaviors around 6-7 months, while in chimpanzees CT is reported to begin around 10 months of age (Robert, 1986). Self-directed behavior has been reported to first emerge in children between 18-24 months of age (Amsterdam, 1972; Anderson, 1984) and in chimpanzees at 4.5 years for some studies (de Veer et al., 2002; Povinelli et al., 1993) and between 28-30 months for other studies (Bard, et al., 2006; Lin, Bard, & Anderson, 1992). This discrepancy in age of onset for chimpanzees may be partly due to the different criteria used to judge self-directed behavior in the Povinelli et al. (1993), de Veer et al. (2002), Lin et al. (1992), and Bard et al. (2006) studies. From the previous descriptions of the mark tests, it is apparent that some debate also exists over discrepancies between human and chimpanzee studies of MSR and what
constitutes mark-directed behavior and passing the mark test. It has also been suggested that older chimpanzees may not show interest in the mirror or they may lose interest with age (de Veer et al., 2002; Povinelli et al., 1993), while human interest in mirrors remains throughout life.

The development of MSR in humans is thought to coincide with the development of the capacity for making secondary representations and other indices of self-awareness, such as, empathy and prosocial behavior, embarrassment, pretend play, and socially imitated or synchronous behaviors (Bischof-Köhler, 2012; Kärtner, Keller, Chaudhary, & Yovsi, 2012; Nielsen & Dissanayake, 2004). Gallup was the first to suggest a connection between MSR and empathy (Gallup, 1982). According to Povinelli et al. (1993), initial studies of the Piagetian stages of sensorimotor development in chimpanzees and orangutans suggest that stages 1-4 (these include reflexes, repeated self-oriented actions, object-oriented actions, & goal directed behavior (Dore & Dumas, 1987)) emerge at ages similar to humans; however, stages 5 (tertiary circular reactions-active experimentation) and 6 (symbolic mental representation, which is thought to coincide with MSR in humans) are delayed. They also suggest that the ability to make secondary representations does not develop in chimpanzees until around age 5 (Povinelli et al., 1993).

**MSR in dolphins and other cetaceans.** Gallup (1982) suggested that the capacity for MSR might also be found in other highly social species, such as, dolphins and elephants given their large complex brains, their complex social structure, and reports of empathy in these species. MSR has been investigated in a few cetacean species. The first studies conducted with bottlenose dolphins used a similar approach to that of Gallup (1970); however, they differed in a few important aspects: dolphins remained with their social group during the studies, dolphins were marked multiple times, and dolphins, like children, were not anesthetized during mark
applications, but instead were sham marked as a control (Marino, Reiss, & Gallup, 1994; Marten & Psarakos, 1994, 1995; Sarko, Marino, & Reiss, 2002). These first studies with dolphins were suggestive of MSR, but were inconclusive due to methodological issues. A study of MSR was also conducted with killer whales (*Orcinus orca*) and false killer whales (*Pseudorca crassidens*) and although the authors state that killer whales exhibited contingency-testing and possibly self-directed behaviors, they have yet to successfully pass the mark test (Delfour & Marten, 2001). A more recent publication described the responses of wild Atlantic spotted dolphins (*Stenella frontalis*) to an underwater mirror (Delfour & Herzing, 2013). The dolphins exhibited very little interest in the mirror and instead of stationing, the dolphins circled the mirror and no contingency-checking behaviors were observed (Delfour & Herzing, 2013).

In the one conclusive study of MSR that has been conducted with bottlenose dolphins (Reiss & Marino, 2001), both individuals tested, two captive born dolphins 13 and 17 years of age, passed the mark test. The dolphins’ behaviors were recorded during several experimental (presence of the mirror) and control (absence of the mirror) conditions: during each of these conditions the dolphins were either marked, sham marked, or not marked. Dolphins, being non-handed and thus unable to touch the mark, were marked multiple times on different parts of their body and the criteria for passing the mark test required that the animal orient the marked part of their body towards the mirror after being marked. Results from this study indicated that dolphins go through similar stages throughout mirror exposure, as reported with children and chimpanzees, with the exception of showing social behavior as these dolphins were not naïve to reflective surfaces. The dolphins exhibited strikingly similar mirror-mediated behaviors (i.e. repetitive body movements, open mouth & close eye viewing, & bubble production) as previously described in humans and the great apes (Reiss & Marino, 2001; Sarko et al., 2002).
Several studies on mirror self-recognition have reported animals producing bubbles in front of the mirror, including chimpanzees, dolphins and killer whales (Delfour & Marten, 2001; Gallup, 1970; Reiss & Marino, 2001; Sarko, et al., 2002). Mirror-directed bubble production is considered to be self-directed and therefore may be evidence for using the mirror as a tool for self-monitoring. Dolphins voluntarily produce various types of bubbles in contexts of both play (Delfour & Aulagnier, 1997; Gewalt, 1989; Kuczaj, Makecha, Trone, Paulos & Ramos, 2006; Marten, Shariff, Psarakos, & White, 1996; McCowan, Marino, Vance, Walke, & Reiss, 2000; Pace, 2000; Reiss, 1988; Paulos, Trone, & Kuczaj, 2010; Tizzi, Castellano, & Pace, 2000) and foraging (Fertl & Wilson, 1997; Fertl & Würsig, 1995; Zaeschmar, Dwyer, & Stockin, 2013), suggesting varying degrees of motivation on the part of the dolphin performing this behavior. A more in depth discussion of bubble play in dolphins will be given later.

Natural history and past cognitive research with dolphins

Dolphins, porpoises and other cetaceans, marine mammals that survive solely in an aquatic environment, diverged from land dwelling mammals approximately 52 million years ago (Butti, Raghanti, Sherwood, & Hof, 2011). Cetaceans have evolved traits that enable them to deal with life in an aquatic environment. For example, the nares are valvular - they remain closed while the muscles are relaxed and open when the muscles are contracted when taking a breath. During their evolution from a land dwelling to a totally marine mammal, the location of the blowhole in cetaceans has migrated to the dorsal portion of the skull, resulting in anatomical changes to the brain (Butti et al, 2011; Reidenberg, 2007). They have also evolved a fusiform shaped body, collapsible lungs and ribcage to deal with high pressure levels that accompany deep dives, pectoral fins containing bones homologous to the forelimbs of terrestrial mammals, the disappearance of hind limbs and the appearance of the fluke to propel them through the
water, and several physiological adaptations that allow them to deal with changing temperatures, buoyancy, and salinity issues (Reidenberg, 2007). Members of the suborder Odontoceti (toothed whales and dolphins) have evolved nasal structures that allow them to produce echolocation clicks used to explore their environment and to locate objects (i.e. prey) and they have highly sensitive hearing (Kellogg, Kohler, & Morris, 1953; Reidenberg, 2007; Roitblat, 2002).

Bottlenose dolphins (*Tursiops truncatus*) are found all over the world in both coastal and pelagic waters and are one of the most widely studied cetacean species both in the wild and captivity (Connor, Wells, Mann, & Read, 2000; Marino et al., 2007). Bottlenose dolphins are considered a long-lived species (approximately 50 yrs) with a 12-month gestation period. Females and their calves form strong bonds, they exhibit synchronized behaviors, frequent physical contact, and females typically nurse their young an average of 3-4 years. Both males and females exhibit delayed reproduction characterized by an extended juvenile or adolescent period (Connor et al., 2000; Connor & Mann, 2006). It has been suggested that delayed reproduction may increase opportunities for learning social skills and foraging techniques (Connor et al., 2000; Herman, 2002).

Due to the demands of aquatic life, bottlenose dolphin calves appear precocious with respect to motor development. In their first days of life dolphin calves must learn to synchronize and control their breaths and before their first month of age they are already demonstrating various behavioral displays and are engaging in playful interactions both alone and with others (Connor et al., 2000; Mann & Smuts, 1999). A study comparing the development of three types of play behaviors (social, bubble & object) in a female captive dolphin calf demonstrated that social play emerged within the first 2 weeks of life, while bubble play was noted within the first month and object play emerged by 2 months of age (Tizzi et al., 2000). Mann & Smuts (1999)
observed social play in wild bottlenose dolphins by the end of week one and by one month they had observed dolphin calves engaging in games of chase and sea grass play.

As opportunistic foragers, bottlenose dolphins of different populations and subsets of the same population exhibit a variety of cooperative and/or solitary foraging strategies. For example, a subset of dolphins in Shark Bay, Australia demonstrate sponging behavior, a solitary foraging strategy in which dolphins uproot marine sponges and hold the sponges over their rostrum while sifting for prey on the ocean floor (Connor & Mann, 2006; Smolker, Richards, Connor, Mann, & Berggren, 1997). This socially learned foraging behavior is unique to this group of dolphins and is considered to be both a form of tool-use and a cultural tradition. Interestingly, other dolphins in the same population are known to beach themselves to capture prey (Sargeant, Mann, Berggren, & Krützen, 2005), a foraging technique reportedly used by other dolphin populations as well. Sub-groups of a population of bottlenose dolphins in Bull Creek, SC cooperate to catch prey by “strand feeding,” which involves a group of dolphins synchronously hauling themselves up onto the muddy shore and feeding on the fish that were beached by their waves (Petricig, 1993, as cited in Duffy-Echevarria, Connor, & St. Aubin, 2008).

Evidence also exists for wild dolphins cooperating with other species during foraging. A recent study reported interspecific cooperative foraging among bottlenose dolphins and false killer whales in New Zealand; both species where observed circling and using bubble bursts to herd fish into tight “balls” up to the surface (Zaeschmar et al., 2013). Bottlenose dolphins have also been shown to engage in cooperative foraging with humans. Several studies have reported a mutualistic relationship between dolphins and local fisherman in Brazil when foraging for mullet (Pryor, Lindbergh, Lindbergh, & Milano, 1990; Simões-Lopes, Fabián, & Meneghetti, 1998). Dolphins herd fish towards fisherman that are standing in the water waiting for a stereotyped
behavioral signal (e.g. head slap, tail slap, or back presentation) from the dolphins before releasing their nets. Once the nets are released the dolphins catch the fish as they try to escape the net (Pryor et al., 1990; Simões-Lopes et al., 1998).

The social structure of bottlenose dolphin societies is extremely complex. Extensive long-term field studies of bottlenose dolphins in Shark Bay, Australia and Sarasota Bay, FL have revealed that dolphins live in open fission-fusion societies with mean group sizes of 5 to 140 that surpass the complexity of those previously described in chimpanzees (Connor et al., 2000; Connor, Watson-Capps, Sherwin, & Krützen, 2011; Lehmann, Korstjens, & Dunbar, 2007). In a fission-fusion society a large community divides into flexible subgroups of varying sizes and membership composition (Lehmann et al., 2007). In bottlenose dolphins these subgroups are typically sex- and age-specific (male-male, female-female, mother-calf) and the size and membership of each subgroup can change daily or even hourly depending on the social context (Connor et al., 2000; Connor & Mann, 2006). It should be noted that there are some individuals that often remain solitary and do not become stable members of subgroups.

Mothers and their calves form nursery groups with other mother-calf dyads; as a result, from a very young age dolphin calves have the opportunity to associate with sometimes as many as 30 other dolphins within their first 2 months of life (Mann & Smuts, 1999). Because males and females remain in their natal range as adults (Connor et al., 2000; Tsai & Mann, 2012) these associations facilitate building bonds that will last into adulthood. A few years after weaning, mother-calf associations decrease significantly, especially for males, while same sex associations with other dolphins increase (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Tsai & Mann, 2012). Throughout their lifetime adult females associate with a large number of individuals (comparable in numbers to primate societies), but they tend to form small dynamic subgroups
with other females that share a similar reproductive status (Connor et al., 2000). For females, the main benefit of being part of a subgroup is defense against predators, but some females have also been seen cooperating against males that are trying to coerce or herd a female group member (Connor et al., 2000).

Male-male subgroups are comprised of 2-3 individuals that typically form long lasting alliances (first order alliance) and they cooperate with each other in herding females for mating opportunities. Notably, bottlenose dolphins also form second order alliances where two or more first order alliances will cooperate in defense against other alliances that are trying to steal females or they will cooperate to try to steal females from other alliances (Connor et al., 2000; Connor & Mann, 2006). More recently, third order alliances have also been described in the bottlenose dolphins that reside in Shark Bay, Australia (Connor et al., 2011). Apart from humans, this level of alliance formation is rare in the animal world.

**The dolphin brain and dolphin cognition**

The ancestral species of cetaceans and primates are thought to have diverged approximately 90-95 million years ago (Marino, 2002; Marino et al., 2007), yet there is sufficient evidence (described above) for behavioral similarities between these groups and as I will describe in the following section, they demonstrate similar cognitive abilities as well.

**Brain structure.** Cetaceans and primates, two evolutionarily divergent groups, demonstrate a remarkable degree of cognitive convergence despite differences in anatomical features of the brain. As previously mentioned, adaptation to life in a fully aquatic environment has lead to several morphological changes, including the structure of the cetacean skull. As evidenced by fossils, changes in the anatomy of the cetacean brain also occurred. Cetacean brains are wider laterally and have shortened along the rostral-caudal axis (Butti et al., 2011).
Cetaceans have the largest brains in absolute size and they have more extensive cortical folds throughout the neocortex than other mammals, but their neocortex is much thinner than that of humans (Butti et al., 2011; Herman, 2002; Marino, 2004; Marino et al., 2007). Cetaceans have a larger cerebellum (relative to brain size) than all primates and their auditory system is highly developed; however, the olfactory system is extremely reduced if not completely absent, the hippocampal formation is also reduced, and the frontal lobes are absent (Butti et al., 2011; Marino, 2004). Finally, the organization of the cetacean cortex is very different from that of a primate brain because the primary somatosensory, motor, visual, & auditory cortices are located adjacent to each other and are not separated by association cortex as in the primate brain (Butti et al., 2011; Marino, 2004). One can also see differences in organization at the cellular level. Cetacean neocortex does not have a granular appearance most likely because it is lacking a granular layer IV (Butti et al., 2011; Marino, 2004).

Despite these differences, primates and cetaceans, specifically Odontocetes, the toothed cetaceans, demonstrate the following similarities: the evolution of large brains with extensive cortical folds, a large cerebral cortex, a high degree of encephalization - larger brain mass then expected relative to body mass, a large amygdala, high ratios of glial cells to neurons – important for rapid efficient neural communication, a large number of von Economo neurons (VENs) - thought to be important for social cognition, and molecular correlates (low level of protein coding substitution rates) (Boddy et al., 2012; Butti et al., 2011; Marino, 2004; Marino et al., 2007; McGowen, Grossman, & Wildman, 2012). A recent phylogenetic analysis of brain size, body size and encephalization quotient (EQ) demonstrated that both primates and cetaceans include species with both the lowest and highest (anthropoid & odontocete) EQ values (Boddy et al., 2012). Although humans (EQ = 7.4 - 7.8) are the most encephalized species, if one compares
the EQ of odontocetes and non-human primates, the relative brain size of bottlenose dolphins (EQ = 4.14) is greater than all non-human primates (great apes EQ = 1.5 - 3) (Boddy, et al., 2012; Herman, 2002; Marino, 2002, 2004). Other species that demonstrate the capacity for MSR have an EQ comparable to the great apes (elephants EQ = 1.13-2.36) (Shoshani, Kupsky, & Marchant, 2006).

It has been suggested that cognitive convergence between great apes and cetaceans is a result of selection pressures placed on animals that need to negotiate dynamic social relationships encountered when living in cognitively demanding social systems (Connor et al., 2000; Connor & Mann, 2006; Herman, 2002). For example, individuals need to decide when it is best to cooperate or when they should compete with conspecifics (Herman, 2012). The idea that the social life of primates was a driving force in the evolution of advanced primate intelligence was first suggested by Jolly (1966) from her studies of lemur social behavior. Humphrey (1976) later corroborated this idea of social intelligence stating, “social skill goes hand in hand with intellect (p. 309).” This social intelligence hypothesis states that the challenges of living in a complex social system require larger brains and advanced levels of intelligence (Holekamp, 2007). Evidence of fission-fusion societies similar to and often surpassing those described in chimpanzee and evidence for third order alliances in wild bottlenose dolphins favors the social intelligence hypothesis as an explanation for the evolution of large complex brains and enhanced cognitive abilities (Connor & Mann, 2006).

**Cognitive abilities of bottlenose dolphins.** Captive studies of bottlenose dolphins have confirmed that they exhibit a wide range of advanced cognitive abilities once thought to be unique to humans and other primates. Studies on dolphin working memory have demonstrated that they have extensive auditory, visual, and spatial memory comparable to non-human primates.
(Herman, 2002; 2010; Marino et al., 2008; Reiss, McCowan, & Marino, 1997). Not only are dolphins capable of visual discriminations both in and out of water, but they also are capable of discriminating between objects of different sizes, shapes, and materials using only echolocation (Marino et al., 2008; Pack & Herman, 1995; Turner & Norris, 1966). Dolphins have been known to imitate both behaviors and vocalizations of conspecifics, via social learning (Herman, 2002; 2010), to spontaneously and rapidly imitate and produce facsimiles of computer-generated whistles and demonstrate evidence for vocal learning (Reiss & McCowan, 1993; Reiss et al., 1997). Much of dolphin behavior, including their complex vocal repertoire, is learned socially. In the wild evidence exists for culture and tool-use in the sponging behavior of Shark Bay bottlenose dolphins (Smolker et al., 1997) and some populations of dolphins may demonstrate dialects in whistle type and structure (Reiss et al., 1997).

There have been extensive studies of the capacity of dolphins to comprehend symbolic communication (an artificial language based on hand gestures) and results demonstrated that dolphins are not only capable of understanding the semantics or representation of each gesture, but they can also process simple syntactic information (Herman, 2002; 2010). Using a different approach to investigate vocal learning and other cognitive capacities in dolphins, Reiss and McCowan (1993) exposed a social group (two mother-young pairs) of dolphins to an underwater keyboard with three-dimensional graphic forms, which provided them with some degree of choice and control in obtaining specific contingencies. By using a free-choice methodology the dolphins were able to freely explore and interact with the keyboard. The dolphins’ use of keys displaying individual graphic forms was followed by their exposure to a specific acoustic signal (a computer generated whistle) and presentation of the specific corresponding objects and activities (Reiss & McCowan, 1993). They also exhibited spontaneous vocal imitation of the
novel sounds (computer-generated whistles) and began to spontaneously produce facsimiles of the sounds in the proper context (Reiss & McCowan, 1993). The dolphins spontaneously (without training) formed learned associations between the temporally related items - the graphic forms, the acoustic signals, the corresponding objects and activities - and exhibited self-organized learning (Reiss & McCowan, 1993).

Previous studies have demonstrated that dolphins have a mental representation of their body image (Herman, 2002; 2012), which according to Anderson (1984) is a requirement for passing the mark test in MSR studies. Studies conducted with captive dolphins have demonstrated that they are capable of learning that specific gestures represent specific body parts and can subsequently follow instructions about what to do with their body parts while interacting with items in their pool (Herman, Matus, Herman, Ivancic, & Pack, 2001; Herman, 2012). Notably, children demonstrate a similar understanding at about 2 years of age (Herman, 2012), also the time when MSR emerges. Not only do dolphins have mental representations of their body, but self-imitation and social imitation studies have shown that they also demonstrate a conscious awareness and conscious control over their body, which suggests that they have a sense of ownership and agency (Herman, 2002; 2012). Again, studies with captive dolphins concluded that when given the instruction “repeat” they copied their own actions that were either previously instructed by the trainer or chosen by the dolphin (via the gesture “create”), even after a 1½ minute delay (Herman, 2012). Results of a recent study that asked dolphins to “vary” their behavior instead of repeat it, confirms that dolphins have mental representations of their past actions (Kuczaj & Eskelinen, 2014).

As previously mentioned, both wild and captive dolphins are social learners and exhibit synchronous behaviors and social imitation as well, which one could argue requires an awareness
of the body and behaviors of others. Dolphins have been shown to mimic the behaviors of other dolphins as well as humans (Herman, 2002; 2012). Being able to mimic the motor actions of humans, a species that is anatomically different from dolphins, with analogous body parts is quite impressive. In a recent study using playbacks of individual ‘signature whistles’ of dolphins, long-term social recognition in dolphins was demonstrated as dolphins were able to remember whistles of prior social group members for up to 20 years (Bruck, 2013). These results showed a significantly higher response rate towards familiar whistles than unfamiliar whistles, which is additional evidence that dolphins are aware of others that they have interacted with socially.

It has been suggested that highly social animals, such as dolphins, that are capable of developing an awareness of self and others may also show evidence of reciprocal altruism (Connor & Norris, 1982). Using different models of reciprocity, Connor & Norris (1982) determined that the characteristics (i.e. mutual assistance in care giving for both the young or injured adults, assistance with defense against predators, cooperative feeding, & behavioral flexibility) that coincide with living in complex fission-fusion societies, have afforded dolphins greater opportunities for engaging in reciprocal altruism and have even encouraged these types of behavioral interactions.

As previously discussed, it has also been documented that bottlenose dolphins are capable of higher order cognitive abilities such as MSR (Reiss & Marino, 2001). In the above background on bottlenose dolphins, several characteristics that make dolphins good candidates for further studies of MSR have been discussed. Dolphins have a highly complex social structure that rivals even that of chimpanzees, have evolved large brains with extensive cortical folds and a large cerebral cortex, and exhibit a wide range of advanced cognitive abilities comparable to the great apes. Although conclusive evidence exists for MSR in dolphins, the age at which it
emerges has not been determined. Studying captive populations of various aged dolphins would present the unique opportunity to describe the age MSR first emerges in this large-brained highly social species and would allow for comparative developmental studies of MSR.
The present study: Age-related aspects of mirror-use by bottlenose dolphins

This research is the first comprehensive study of the developmental and other age-related aspects of MSR in a social group of three generations of captive bottlenose dolphins at the National Aquarium, Baltimore, MD. During a longitudinal study, conducted over a 3-year period, I collected behavioral data on the responses of various aged dolphins during mirror exposure (the first year’s data was collected by my thesis advisor, Diana Reiss). I conducted a detailed continuous event-based analysis of video recordings to describe and quantify three dolphins’ (Bayley, Foster, & Nani) vocal and behavioral responses to the mirror, noting the presence of patterns that arise with the emergence of MSR in order to make comparisons with MSR data previously described in humans and chimpanzees.

Aims and predictions

The aims of this study were to: 1) test dolphins of various ages and further confirm the capacity for MSR in this species, 2) describe the age at which MSR emerges in bottlenose dolphins, 3) observe when the stages of behavior emerge and quantify specific mirror-mediated behaviors exhibited by each dolphin throughout mirror exposure, and 4) compare the developmental dolphin data with data previously described in humans and chimpanzees. Based on previous research (Reiss & Marino, 2001) it was expected that the dolphins in this study would demonstrate the ability for MSR. Due to the demands of living in a fully aquatic environment and the consequent precocious motor development of bottlenose dolphin calves and their complex social bonds, it was also predicted that MSR would emerge in dolphins at an age comparable to that seen in humans and chimpanzees.
Method

Subjects and facilities

A three-generational social group of nine bottlenose dolphins (*Tursiops truncatus*) from the National Aquarium, Baltimore, MD were exposed to a mirror over a 3-year period. The social group was comprised of two males: Foster (DOB 9/9/07, son of Jade), Beau (DOB 6/27/05, son of Nani) and seven females: Bayley (DOB 7/27/08, daughter of Chesapeake), Spirit (DOB 4/13/01, daughter of Nani), Maya (DOB 5/13/01, daughter of Shiloh), Jade (DOB 5/22/99), Chesapeake (DOB 3/7/92, daughter of Shiloh), Shiloh (~DOB 1979, died 2010) and Nani (~DOB 1972). This study examined the earliest age that dolphins begin to show self-directed behavior and focused on the two youngest dolphins (Bayley & Foster) and questioned if older dolphins still show interest in the mirror by focusing on the behavior of the oldest dolphin (Nani).

The dolphins resided in sub-groups that were housed in four separate and interconnected pools. Based on husbandry decisions, the composition of these sub-groups changed periodically throughout the study. The exhibition pool (EP), the largest of the four (100 ft (30.5 m) across x 50 ft (15.2 m) wide x 24 ft (7.3 m) deep), is connected to both HP1 (60 ft (18.3 m) in diameter x 15 ft (4.6 m) deep) and HP2 (50 ft (15.2 m) in diameter x 12 ft (3.7 m) deep) by two separate gates and these two pools connect to a small medical pool. The EP pool has multiple underwater windows for public viewing (see Figure 1). Located in a central location between the EP, HP1 and HP2 pools is an additional underwater viewing area called “the pit”. This area is a small circular room (~4 ft across) that is accessed by descending a vertical ladder. Within the pit, there are three windows, one into each of the EP, HP1 and HP2 pools. This area is not accessible by the public and can only be accessed by staff and research personnel. It is important to note that
the differential and changing light levels between the dolphin pools and exterior observation areas can result in mirror-like reflectivity on the poolside of the window surfaces. Thus, due to the large number of potentially reflective surfaces (windows) surrounding the exhibition pool and the underwater viewing windows in the pit, the dolphins should not be considered mirror naïve at the onset of the study.

*Figure 1. Image of the dolphin facility at the National Aquarium, Baltimore, MD*

**Procedures**

A similar methodology for mirror exposure used in a previous study of MSR in dolphins (Reiss & Marino, 2001) was followed. Using a Canon HV20 HD video camera, recordings of the behavior of various aged dolphins in the social group were conducted under three conditions: a two-way mirror (experimental), window only (baseline), and a non-reflective surface (control). Sessions were conducted during a period from November 21, 2008 through December 15, 2011
for 1 hour, 1 to 2 days a week, biweekly. However, due to husbandry activities and other unforeseen projects at the facility, there were times when sessions could not be conducted. Baseline and control sessions were interspersed between experimental sessions. All sessions were conducted from the underwater viewing windows inside the pit between the 3 main pools at approximately 9am, which was before the exhibit was open to the public. On occasion, due to scheduling issues some sessions were conducted late morning and were shorter than 1 hour in duration. The number of dolphins present during each session varied over the course of the study due to husbandry decisions based on the social dynamics.

**Experimental/mirror sessions.** We used a two-way mirror which presented a reflective mirror surface facing the dolphin side of the pool and a transparent surface facing the inside of the pit that allowed us to observe the dolphins’ behavior at the mirror without them being aware of our presence. To create an optimal two-way mirror, it was necessary to darken the non-mirror side facing into the pit by covering the remaining two windows of the non-experimental pools, which housed the other dolphins and closing the overhead hatch of the pit. The windows were covered with white opaque poster board (white was used to minimize the reflective property of the glass for the dolphins in the other pools). The windows were also covered in dark velour curtains. At the onset of each session, video recording began and then the two-way mirror was secured to the top and bottom of the viewing window with a strip of duct tape. A rolled black cloth was placed along the lower edge of the mirror to insure that there was no visibility into the pit below the mirror. A researcher and a member of the dolphin care staff observed from seated positions in the pit and quietly took notes on the identity of the dolphins at the mirror, the time they arrived at the mirror, and their subsequent behavior. All experimental sessions were videotaped from the pit and the camera was positioned on a tripod approximately 4 ft (1.2 m)
from the window into HP1 (only a few sessions were conducted in HP2). Neither the camera nor the researchers were visible to the dolphins during sessions.

**Mark test sessions.** Once we determined that the dolphins were exhibiting self-directed behavior, we conducted a series of mark test and sham mark test sessions. During these sessions, the dolphins were exposed to the mirror for approximately 15-minutes and then the trainers signaled them to station at the opposite side of the pool from the mirror. A single dolphin was marked with a triangle or “X” by their trainers, using either a black non-toxic marker or black lipstick, on various parts of their body that they could not see without the use of the mirror. The markers that were initially used did not produce reliable or consistent marks and were replaced in later sessions with black lipstick. Specifically, the dolphins were marked on either side of their head behind their eye, on the inside of one of their pectoral fins, or on their ventral surface between their pectoral fins. For sham mark sessions, dolphins were marked using a water-filled marker, which does not leave a visual mark. After the mark was applied, the marked dolphin and other dolphins were released from station and video recordings continued to document the dolphins’ behaviors at the mirror. During these sessions, the researchers in the pit noted the time of stationing (when the dolphin was marked), the time of release, and their subsequent behavior at the mirror. In this study, instead of conducting mark test sessions once self-directed behavior was observed, mark tests were delayed due to husbandry concerns by the animal care staff about handling and marking dolphins at such young ages.

**Baseline sessions.** Baseline sessions were conducted to determine the dolphins’ behaviors at the window in the absence of the mirror. These sessions were videotaped in the same manner as the experimental sessions, but the two windows into the non-experimental pools remained uncovered, the pit hatch remained open, and the two-way mirror was absent. It was
important to note that during baseline sessions the pit area was not dark in order to minimize the reflective properties of the window itself. Because the dolphins were able to see into the pit through the window and our presence would potentially affect their behavior, the video camera was set up and started and then the researcher immediately left the pit area until the termination of the session. Due to husbandry decisions, the subgroups of dolphins in the pools during baseline conditions was not always consistent; however, only dolphins that participated in the mirror study were in the pool during this condition.

**Control sessions.** To control for the placement of a novel object (the mirror) onto the window, a non-reflective clear surface (Plexiglas) was affixed to the window and video recordings were conducted. After 3 sessions it was determined that the Plexiglas itself was reflective when mounted against the window surface and we discontinued its use. Instead, we used a 1 inch-wide non-reflective matt black poster board frame with the same dimensions as the window for the control in the remaining control sessions. The protocol used for the baseline sessions was repeated in the control sessions. Due to husbandry decisions, the subgroups of dolphins in the pools during control conditions was not always consistent; however, only dolphins that participated in the mirror study were in the pool during this condition.

**Data analysis**

Prior to the beginning of the study, to determine the field of visibility at the mirror from the dolphins’ point of view, a diver wearing an underwater communication device linked to a receiver in the pit positioned himself in front of the window in HP2 while the dolphins were held in adjacent pools. From the pit window, the diver’s reflection was videotaped while swimming up to the mirror and orienting from various positions relative to the mirror. The diver
simultaneously informed the researchers in the pit when he could and could not view different parts of his body in the mirror.

Using an ethogram (see Appendix A), a detailed continuous event-based analysis of the dolphins’ video recorded behaviors in the three conditions was conducted for the complete first year of mirror exposure and for video recordings that were sampled from each month for the last 2 years. For the last 2 years of the study, recordings were selected based on one of two criteria: 1. all recordings labeled as mark sessions for Bayley, Foster or Nani were selected and 2. at least one recording from each month, where there appeared to be interest in the mirror, was selected.

The analysis included the identification and quantification of the categorized behaviors exhibited (e.g., exploratory/social behavior, contingency-testing, self-directed, repetitive self-directed, self-directed social, repetitive self-directed social, stationing, or ambiguous) and the duration of time spent at the mirror. Repetitive self-directed behavior included behaviors categorized as self-directed that were being repeated consecutively. Self-directed social behavior included behaviors categorized as social that occurred after the dolphin had reliably demonstrated self-directed behaviors at the mirror. Repetitive self-directed social behavior included self-directed and social behaviors that occurred simultaneously and were repeated consecutively. Stationing is when the dolphin was positioned facing the mirror for more than 3 seconds, but was not engaged in a specific behavior. “Ambiguous” included behaviors that did not clearly fit into one of the other categories. The duration of time spent at the window in the baseline and control conditions was compared with the duration of time spent in front of the mirror in the experimental/mirror conditions. During analysis of the video recordings for the baseline sessions, it was discovered that during 3 of the baseline sessions, aquarium staff had entered the pit and closed the hatch to the pit so these sessions were not included in the analysis.
To account for differences in the number of sessions each dolphin had access to the mirror and the inequality of the durations of each session (not all recordings were an hour long), calculations were performed to transform the data into frequency of behaviors per hour and duration (in seconds) per hour. Comparisons with specific behaviors and stages of behavior at the mirror previously described in dolphins, humans, and chimpanzees were also made.

**Mark test.** Two different observers (Diana Reiss and myself) coded all mark test sessions. During coding of the videotapes, the second observer (Diana Reiss) was blind to where the dolphin was marked and she degraded the image by squinting and focused only on the dolphins’ body movements and orientations. Once all mark test sessions were analyzed, the two observers discussed their findings and determined if they were in agreement. Criteria used for passing the mark test were based on prior work with adult dolphins (Reiss & Marino, 2001): 1) if the dolphin immediately oriented the marked part of their body towards the mirror when first approaching the mirror following application of the mark or 2) if the dolphin oriented the marked part of its body toward the mirror more frequently in the post-mark condition versus the pre-mark condition. Comparisons of the marked dolphin’s behavior during each mark session, prior to the mark and after the mark, were also made to confirm that changes in the dolphin’s behavior were in response to the presence of the mark.

**Mirror-directed bubble behavior.** In order to describe and quantify the types of bubble behavior exhibited in front of the mirror, a pseudo-random subset of the recordings were selected between January 9, 2009 and November 18, 2011. A total of 32 experimental sessions that did not occur in the same week were selected and bubble behavior events were coded using an ethogram of dolphin bubble behavior at the mirror (refer to Appendix B). A bubble behavior event was coded as a single type of bubble(s) or a single type of bubble(s) and the dolphins’
behavioral interaction with the bubble (contact with bubble and/or posture). A research assistant, who was trained to accurately identify the dolphin at the mirror and its subsequent behavior, coded these video recordings. Again, due to the dolphins having unequal amounts of mirror exposure, the dolphins’ rates of bubble production per one-hour session were calculated.

**Results**

Throughout this 3-year longitudinal study, a total of 57 sessions were analyzed for the three dolphins (44 experimental/mirror, 7 baseline, & 6 control) between 11/21/2008 through 12/14/2011. See Table 1 for the dolphins’ ages throughout the study, amount of mirror exposure, and total time spent at the mirror. The following descriptive results include the frequency ($f$) of the observed categorized behaviors and their percentage of the total number of observed categorized behaviors.

Table 1

*Age during mirror exposure, amount of mirror exposure (number of sessions and exposure time) and total time spent at the mirror for each dolphin.*

<table>
<thead>
<tr>
<th>Dolphin</th>
<th>Age</th>
<th>Sessions</th>
<th>Exposure Time</th>
<th>Total Duration at Mirror</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>YY</td>
<td>MM</td>
<td>DD</td>
<td>#</td>
</tr>
<tr>
<td>Bayley</td>
<td>00</td>
<td>03</td>
<td>27</td>
<td>36</td>
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<tr>
<td></td>
<td>03</td>
<td>04</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Foster</td>
<td>00</td>
<td>14</td>
<td>13</td>
<td>35</td>
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<td></td>
<td>04</td>
<td>02</td>
<td>07</td>
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</tr>
<tr>
<td>Nani</td>
<td>37</td>
<td>-</td>
<td>-</td>
<td>23</td>
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<tr>
<td></td>
<td>39</td>
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</tbody>
</table>

*Note:* The month and day of Nani’s birth are unknown. Exposure Time is the amount of time the mirror was present for each session, summed over the number of sessions.
**Frequency and social context of categories of behaviors at mirror**

A detailed behavioral analysis was conducted to categorize and quantify specific types of behaviors or behavioral events exhibited at the mirror by each dolphin. The total frequency of behaviors produced by Foster \((f = 4173)\) was much higher than both Bayley \((f = 897)\) and Nani \((f = 934)\) combined. After normalizing the data by transforming the frequencies into frequency per hour, Foster (130.6 behaviors per hour) still produced more behaviors at the mirror than both Bayley (26.3 behaviors per hour) and Nani (42.3 behaviors per hour). The total frequency of behaviors was calculated and normalized for each dolphin for each day of mirror exposure. To determine if there was a significant difference between the median frequencies of behaviors exhibited by Bayley \((Mdn = 17)\), Foster \((Mdn = 102)\), and Nani \((Mdn = 40)\) at the mirror across all days, a Kruskal-Wallis test was conducted. Results demonstrated that there was a significant difference between the median frequency of behaviors exhibited by the dolphins, \(\chi^2(2, N = 94) = 41.60, p < .001, \eta^2 = .45.\) Mann-Whitney U post hoc tests were conducted to evaluate pairwise differences among the median behavioral frequencies for the three dolphins using a Bonferroni corrected alpha value of 0.017. These tests demonstrated that Foster exhibited significantly more behaviors at the mirror than Bayley, \(U = 116.5, p < .001, r = .70.\) Foster also exhibited significantly more behaviors at the mirror than Nani, \(U = 136.5, p < .001, r = .56.\) Finally, there was also a significant difference between the frequency of behaviors for Nani and Bayley, \(U = 237.0, p = .006, r = .36.\)

Bayley exhibited only 8 (0.9%) episodes of social behavior throughout the entire study, while the majority of her behavior was categorized as self-directed \((f = 356, 39.7\%)\), followed by ambiguous \((f = 242, 27\%)\), stationing \((f = 201, 22.4\%)\), and contingency-testing \((f = 90, 10\%)\). On the first day of mirror exposure when Bayley was almost 4 months old, she spent very little
time at the mirror (46 sec) and the few behaviors she exhibited (e.g. distant stationing, circling, & swim-by's) were categorized as ambiguous ($f = 7, 100\%$). However, no social behavior was observed on day one (see Figure 2).

![Bayley: Frequency of Categorized Behaviors](image)

*Figure 2.* Frequency of Bayley’s categorized behaviors for each day of mirror exposure. The line delineates when Bayley had consistent mirror exposure for an entire year (left) versus samples of less consistent mirror exposure (right). The arrow denotes the first day that Bayley started demonstrating self-directed behavior at the mirror (she was 5½ months old). The shaded sections represents the age when children demonstrate the three stages: social behavior (pink, 4-8 months), contingency-testing (green, 8-12 months), & self-directed (blue, 18-24 months).

On day four of mirror exposure, when Bayley was 5½-mos old, she exhibited predominantly self-directed ($f = 24, 53.3\%$) behavior (e.g. close-eye viewing & bubble production) and very few
contingency-testing \((f = 3, 6.7\%)\) behaviors. Almost half of all of the behavioral events exhibited by Bayley were when she was alone at the mirror \((f = 359, 49.7\%)\). When Bayley and only one other dolphin were at the mirror, the dolphin that was with her most frequently was Foster \((f = 78, 10.8\%)\) followed by Shiloh \((f = 61, 8.4\%)\), but not her mother Chesapeake. The number of behaviors that Bayley produced when she was alone at the mirror versus with others was calculated for each day of mirror exposure and a Wilcoxon Signed-ranks test was conducted. Results demonstrated that there was no significant difference between the number of behaviors Bayley produced while alone at the mirror \((Mdn = 9)\) and the number of behaviors she produced when with other dolphins at the mirror \((Mdn = 8.5)\), \(Z = 0.88, p = .38, r = .15\).

Foster exhibited little social behavior \((f = 388, 9.3\%)\) and the majority of his behavior was categorized as self-directed \((f = 1926, 46.2\%)\) followed by ambiguous \((f = 789, 18.9\%)\), contingency-testing \((f = 664, 16\%)\), and stationing \((f = 406, 9.7\%)\). Notably, on the first day of mirror exposure when Foster was almost 14 \(\frac{1}{2}\) months old, he exhibited predominantly self-directed behavior \((f = 48, 40.7\%)\) marked by close eye viewing, open mouth viewing, and bubble production/play. Contingency-testing, marked by repetitive head and body movements, was also observed but to a lesser degree \((f = 8, 6.8\%)\); little social behavior \(2\) instances of whistle bubble streaming and \(2\) instances of echolocation) was observed \((f = 4, 3.4\%)\) (see Figure 3).
Figure 3. Frequency of Foster’s categorized behaviors for each day of mirror exposure. The line delineates when Foster had consistent mirror exposure for an entire year (left) versus samples of less consistent mirror exposure (right). The shaded section represents the age when children demonstrate self-directed behaviors (18-24 months).

A substantial number of behaviors were exhibited when Foster was alone at the mirror \((f = 3124, 74.9\%)\). The number of behaviors that Foster produced when he was alone at the mirror versus with others was calculated for each day of mirror exposure and a Wilcoxon Signed-ranks test was conducted. Results demonstrated that there was a significant difference between the number of behaviors Foster produced while alone at the mirror \((Md n = 79)\) and the number of behaviors he produced when with other dolphins at the mirror \((Md n = 20)\), \(Z = 5.00, p < .001, r = .85\).
Nani also exhibited very few episodes of social behavior \( (f = 12, 1.3\%) \) throughout the entire study. Almost half of the behaviors exhibited by Nani, while in front of the mirror, were self-directed \( (f = 456, 48.8\%) \) followed by stationing \( (f = 165, 17.7\%) \), ambiguous \( (f = 156, 16.7\%) \), and contingency testing \( (f = 145, 15.5\%) \). More than half of the behaviors exhibited by Nani were when she was alone at the mirror \( (f = 511, 54.7\%) \). When Nani was stationed at the mirror with another dolphin, the dolphin most frequently with her was her son Beau \( (f = 286, 30.6\%) \). As with Foster, on the first day of mirror exposure, Nani exhibited predominantly self-directed behavior \( (f = 26, 53.1\%) \) marked by close eye viewing, open mouth viewing, and head movements. Also, no social behavior was exhibited and very few instances of contingency testing \( (f = 4, 8.2\%) \), marked by repetitive pectoral fin and head movements, were observed (see Figure 4).
Figure 4. Frequency of Nani’s categorized behaviors for each day of mirror exposure. Nani was tested more opportunistically; therefore, she did not have access to the mirror for several months at a time.

The number of behaviors that Nani produced when she was alone at the mirror versus with others was calculated for each day of mirror exposure and a Wilcoxon Signed-ranks test was conducted. Results demonstrated that there was no significant difference between the number of behaviors Nani produced while alone at the mirror ($Mdn = 17$) and the number of behaviors she produced when with other dolphins at the mirror ($Mdn = 13$), $Z = 1.60, p = .11, r = .33$.

A comparison of all three animals shows that their behaviors in front of the mirror were predominantly self-directed (see Figure 5).
Figure 5. Comparison of the frequency of contextual categorized behaviors for each dolphin. Notably, most behaviors were categorized as self-directed and both Bayley and Nani exhibited no social behavior.

Notably, on June 3, 2009, both Foster (aged 1-yr, 8-mos, 14th day of mirror exposure) and Nani (aged 37-yrs, 10th day of mirror exposure) produced their highest daily total of behaviors at the mirror for all days analyzed. This day also marked Foster and Nani’s highest frequencies of self-directed behavior and social behavior. Bayley (aged 1-yr, 3 ½-mos) produced her highest daily
total of behaviors on November 12, 2009 (20th day of mirror exposure), which was marked by her highest frequencies of behaviors categorized as self-directed, ambiguous and contingency testing (see Figures 2-4).

Many of the behaviors initially categorized as social and contingency testing occurred after the dolphins had already been observed demonstrating self-directed behavior in the absence of social behavior and even directly following bouts of self-directed behaviors within a session. As a result, the previous categories were reevaluated and contextual categories were added (repetitive self-directed, self-directed social, & repetitive self-directed social). For Bayley, all repetitive behaviors that occurred within her first four sessions of mirror exposure (1/16/09 and prior) were categorized as contingency-testing because she did not start showing self-directed behaviors until 1/16/09. All other repetitive behaviors exhibited after these dates were categorized as either repetitive self-directed or repetitive self-directed social. For Foster, to be conservative, the same protocol described above for Bayley was used. However, because Foster also exhibited a few social behaviors, any social behaviors exhibited within his first four sessions (1/16/09 and prior) were categorized as social unless they occurred simultaneously with self-directed behaviors, in which case they were categorized as self-directed social. Due to Nani’s age and because she exhibited self-directed behaviors in the absence of social behaviors on her first two days of mirror exposure, only repetitive behaviors exhibited on day 1 (2/5/2009) of mirror exposure were categorized as contingency-testing. Following recategorization, Bayley and Nani’s frequency of social behaviors decreased to zero and there was a considerable decrease in the frequency of social behavior for Foster (from $f = 388$ to $f = 13$). The number of repetitive behaviors categorized as contingency-testing also decreased because much of the repetitive behaviors were occurring in contexts along with self-directed behaviors (see Figures 6a, 6b).
Figure 6. (a) Comparison of the frequency of categorized behaviors exhibited by Bayley, Foster, and Nani. This figure demonstrates a similar trend; all three dolphins exhibited predominately self-directed behavior and very little social behavior. (b) Comparison of the frequency of behaviors exhibited following recategorization using the contextual categories.
Behavioral comparisons: Dolphins, humans, & chimpanzees

The dolphins in this study produced a suite of behaviors previously described in prior MSR studies with humans, chimpanzees, and dolphins (see Table 2).

Table 2

Total frequencies of a subset of specific behaviors scored for each dolphin.

<table>
<thead>
<tr>
<th>Category/Behavior</th>
<th>Bayley</th>
<th>Foster</th>
<th>Nani</th>
</tr>
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<td>Primates &amp; Dolphins</td>
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<td>51</td>
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<td>2.9</td>
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<tr>
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<td>25.3</td>
<td>13.6</td>
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Note: For full descriptions of these behaviors see Appendix A. The term “Primates” includes both humans and chimpanzees. ¹ denotes most frequent behavior, ² denotes second most frequent behavior, ³ denotes third most frequent behavior.
Specifically, while at the mirror, the dolphins in this study exhibited self-directed behaviors including: close eye viewing, open mouth viewing, head and body movements, flexing and contorting body (described in chimpanzees but not humans), somersaulting (described in chimpanzees but not humans), bubble blowing, and interacting with others while using the mirror to monitor these interactions. Nani’s second most frequent behaviors were vertical head movements ($f = 139, 14.9\%$) and Foster’s third most frequent behaviors were wide-open mouths ($f = 788, 18.9\%$). Bubble production was a frequently occurring behavior for all three dolphins: bubble production was Nani’s ($f = 179, 19.2\%$) most frequent behavior and both Foster’s ($f = 1028, 24.6\%$) and Bayley’s ($f = 155, 17.3\%$) second most frequent behaviors. Therefore, a more detailed analysis of mirror-directed bubble behavior will be discussed later.

Similar to other species, dolphins also altered their viewing angle at the mirror by exhibiting behaviors both while distant and when approaching the mirror. These dolphins also exhibited social behaviors at the mirror similar to other species, although social behaviors were not common. For example, head jerking in dolphins is synonymous to head bobbing that has been previously observed in chimpanzees (Gallup, 1970). Although the types of vocalizations observed (i.e. whistling & squawking) in this study are unique to dolphins, both humans and chimpanzees have been observed vocalizing while in front of the mirror (Amsterdam, 1972; Dixon, 1957; Gallup, 1970). In this study, vocalizing while at the mirror was infrequent for both Bayley and Nani and more common for Foster. Notably, almost all vocalizing occurred after the dolphins were exhibiting self-directed behavior in the absence of social behavior. As a result, most vocalizing was categorized as self-directed social. Squawking was observed almost exclusively by Foster; however, Bayley began to exhibit this behavior ($f = 2$) at the mirror when she was a little over 10-months old (6/5/09) and she did not squawk again until she was 2-yrs, 7-
months (2/25/11, \(f = 2\)) and then again when she was 3-yrs, 3-months (11/1/11, \(f = 1\)). Notably, Foster did not vocalize at the mirror during most of the sessions and only started squawking in front of the mirror when he was 1-year, 9-months (6/3/09), which was only two days before Bayley. Squawking continued to be a part of Foster’s behavioral repertoire in front of the mirror and was seen on 13 additional days. However, he produced more squawks (\(f = 217\)) on the two consecutive days this behavior was first observed than on the 11 other days combined (\(f = 168\)). Although infrequent, echolocation, another behavior that is unique to dolphins, was also exhibited almost exclusively by Foster, starting with his first 2 days of mirror exposure and continuing intermittently over an additional 14 days.

The dolphins in this study also produced a suite of self-directed behaviors that are consistent with those previously described in other MSR studies with dolphins (Marten & Psarakos, 1995; Reiss & Marino, 2001; Sarko et al., 2002). For example, barrel rolling was a behavior that all three dolphins exhibited while stationed in front of the mirror. Foster engaged in this behavior more frequently than both Bayley and Nani (see Table 2). These dolphins also exhibited behaviors at the mirror while their body was completely inverted. Again, Foster exhibited this behavior more frequently than both Bayley and Nani, who rarely inverted their body while at the mirror. When inverted, Foster was either stationed or he engaged in various behaviors simultaneously; such as, bubble production, head movements, vocalizing, close eye viewing, and open mouth viewing.

All of the dolphins in this study produced behaviors that involved making contact with the surface of the mirror. Other species have also been described making contact with the mirror; however, dolphins exhibit unique behaviors. These behaviors include: head butting the mirror (with (HBBP) & without producing bubbles (HB)), sliding the ventral surface of their body
along the window where the mirror is located (BSW), and rostrum contact (RC). Head butt and rostrum contact on their own were considered ambiguous; however, these were two of the most frequently occurring behaviors. Head butt was Bayley’s most frequent behavior ($f = 184, 20.5\%$) and although it was not one of Foster’s top three most frequent behaviors, Foster exhibited HB ($f = 462, 11.1\%$) more often than both Bayley and Nani ($f = 69, 7.4\%$). Rostrum contact was observed by all three dolphins often and was Foster’s ($f = 1055, 25.3\%$) most frequent behavior and Bayley’s ($f = 86, 9.6\%$) and Nani’s ($f = 127, 13.6\%$) third most frequent behavior. The dolphins produced HB and RC in multiple orientations (head-on, left, right, & inverted) and also simultaneously. On some occasions, the dolphins would HB the mirror and then rub their rostrum along the glass as they moved their head up again. BSW was almost exclusively produced by Foster; however, Bayley also produced this behavior twice.

**Turn taking and synchronous behaviors at the mirror.**

Because the dolphins in this study were exposed to the mirror when they were in social groups, they had ample opportunities to interact with each other while at the mirror and to use the mirror as a tool to view these interactions. Some of these interactions included engaging in synchronous (often dyadic interaction where dolphins perform similar behaviors in unison) and turn taking (dyadic interaction where dolphins perform similar behaviors one after the other) behaviors while at the mirror. For example, head butting the mirror was also done in unison with other dolphins. On three separate occasions, Foster and Beau approached the mirror and took turns head butting. During 5 different bouts Foster and Beau not only performed head butts but they also floated back away from the mirror in the same plane (HBNF). This would continue and each dolphin would take turns consecutively swimming back towards the mirror to head butt and then float backwards, stationing and watching the mirror as the other dolphin proceeded to head
butt. During one specific bout of head butt turn taking, Foster and Beau repeatedly head butted the mirror 14 times in a row. This behavior also increased in complexity by adding a bubble production after the head butt, which was seen in a bout of turn taking involving Bayley and Foster.

A type of synchronous behavior seen between Foster and Bayley was repeated circling in front of the mirror. When circling both dolphins circled at the same time positioned one in front of the other. This was seen on 5 different occasions and during one of these bouts both Foster and Bayley circled 8 times in a row. One bout of repeated circling was also seen between Foster and Beau. There was also one instance of what appeared to be synchronous repeated head rotations by Foster and Beau. Foster was at the mirror repeatedly rotating his head, while behind him, more distant, Beau was swimming up to the mirror doing the same head rotations.

**Mirror-directed bubble behavior**

For Bayley, Foster, and Nani combined, there were a total of 1070 bubble behavior events. The most frequently observed bubble behavior events were multiple bubbles (BM) ($f = 336, 31.4\%$) followed by bubble bursts (BB) ($f = 287, 26.8\%$) and bubble streams (BS) ($f = 157, 14.7\%$) (see Figure 7).
Figure 7. Comparison of the frequency of bubble production by each dolphin per day. For almost all of the days, Foster produced the highest number of bubble behavior events. Notably, on June 3, 2009, both Nani and Foster produced their highest level of bubble behavior events, which coincides with the day they spent the longest durations at the mirror and produced the most mirror-mediated behaviors.

Foster bubbled most frequently ($f = 754, 70.5\%$), followed by Bayley ($f = 187, 17.5\%$) and then Nani ($f = 129, 12.1\%$). Foster was the only dolphin observed creating all 18 (100%) bubble behavior variations listed on the ethogram. Bayley produced more than half of the variations ($f = 11, 61.1\%$), while Nani produced the least ($f = 7, 38.9\%$). There was one session in which there was a noticeable increase in bubble production (June 3, 2009) ($f = 253, 23.6\%$), which coincides with Foster’s highest duration of time spent at the mirror and his highest daily frequency of behavioral events produced (see Figure 8).
Figure 8. The total frequency (Bayley, Foster, & Nani combined) of each bubble behavior event. The most frequent bubble behavior event exhibited was multiple bubbles ($f = 336, 31.4\%$), followed by bubble bursts ($f = 287, 26.8\%$) and bubble streams ($f = 157, 14.7\%$).

Dolphins were observed producing bubble behaviors in front of the mirror both when alone and when other dolphins were also at the mirror. Bayley ($f = 136, 72.7\%$) and Foster ($f = 617, 81.8\%$) produced more bubbles in front of the mirror when alone. Nani ($f = 87, 67.4\%$) produced more bubbles when at the mirror with other dolphins. Notably, 53.5\% of Nani’s bubble behaviors were produced while her male offspring Beau, aged 3-years, 5-months at the onset of the study, was also at the mirror. As previously stated, 30.6\% of Nani’s total behaviors were performed while at the mirror with Beau.
Duration of time spent at mirror

An analysis of total duration of time spent at the mirror showed that Foster (19,658 sec) spent considerably more time at the mirror than both Bayley (4,146 sec) and Nani (4,568 sec) combined; however, Bayley and Nani spent comparable amounts of time at the mirror. To control for the differences in the amount of mirror exposure between the three dolphins, the amount of time spent at the mirror was transformed to duration per hour. Consistent with the total durations, Foster spent more time at the mirror (561.7 sec per hour) than both Bayley (115.2 sec per hour) and Nani (198.6 sec per hour). Bayley, the youngest dolphin, had the highest level of mirror exposure (36 sessions); however, she spent the least amount of time in front of the mirror. Nani, the oldest dolphin, had much less mirror exposure than Bayley, yet she spent more time at the mirror and as was previously shown, produced a higher frequency of behaviors at the mirror than Bayley. A Kruskal-Wallis test was conducted to determine if there was a significant difference between the median duration of time the dolphins spent at the mirror. Results demonstrated that there was a significant difference between the median duration of time spent in front of the mirror by Bayley ($Mdn = 82$), Foster ($Mdn = 427$), and Nani ($Mdn = 211$), $\chi^2(2, N = 94) = 42.52$, $p < .001$, $\eta^2 = .46$ (see Figure 9). Mann-Whitney U post hoc tests were conducted to determine pairwise differences among the median durations for the three dolphins. For these tests a Bonferroni corrected alpha value of 0.017 was used. These tests demonstrated that Foster spent significantly more time at the mirror than Bayley, $U = 112$, $p < .001$, $r = .71$. Foster also spent significantly more time at the mirror than Nani, $U = 138.5$, $p < .001$, $r = .55$. Finally, there was also a significant difference between the durations for Nani and Bayley, $U = 224$, $p = .003$, $r = .38$. 
Figure 9. Comparison of the total duration of time that each dolphin spent in front of the mirror. The durations were normalized across each day to account for differences in mirror exposure time and then summed for each dolphin. Foster spent significantly more time at the mirror than both Bayley and Nani, while Nani spent significantly more time at the mirror than Bayley.

As expected, all of the dolphins’ highest durations/hour occurred on the days when their most frequent behavioral events were observed (June 3, 2009 for Foster & Nani, November 11, 2009 for Bayley) (see Figure 10).
Figure 10. Comparison of the duration of time each dolphin spent at the mirror per day. Some of the sessions were less than 1 hour; therefore, the durations were transformed into duration per hour. The line delineates when the first year of consistent mirror exposure ended for Bayley and Foster. The values to the right of the line were sessions sampled from years two and three.

The duration of time spent stationing at the window was calculated for each of the baseline and control sessions. To control for differences in the number of sessions for each condition, the overall durations for each condition were transformed into amount of time spent at the window per hour (see Figure 11).
Figure 11. Comparison of the total (Bayley, Foster, & Nani combined) rate of time spent at the window per hour between each condition. The dolphins spent significantly more time at the mirror during the experimental condition than they did at the window in the both the baseline and control conditions.

To determine if there was a difference between the median duration of time the dolphins spent stationing at the window during the baseline, control, and mirror conditions, a Kruskal-Wallis test was performed. Results demonstrated that there was a significant difference between the median duration of time spent in front of the mirror/window during the experimental ($Mdn = 212$), baseline ($Mdn = 0$), and control ($Mdn = 28$) conditions, $\chi^2(2, N = 127) = 53.75, p < .001$, $\eta^2 = .43$. Mann-Whitney U post hoc tests were conducted with a Bonferroni corrected alpha value of 0.017. These tests demonstrated that the dolphins spent significantly more time at the window during the mirror condition than the baseline condition, $U = 89, p < .001, r = .55$. The
dolphins also spent significantly more time at the window during the mirror condition than the control condition, $U = 137.5$, $p < .001$, $r = .50$. Finally, there was no significant difference between the durations for the baseline condition and the control condition, $U = 90$, $p = .07$, $r = .31$. Two additional Kruskal-Wallis tests were also conducted to determine if there was a difference among the dolphins in time spent at the window in the baseline condition and also in the control condition. Results demonstrated that there was no significant difference among them in regards to time spent in front of the window in the baseline condition ($\chi^2(2, N = 17) = 0.41$, $p = 0.82$, $\eta^2 = .03$) or in the control condition ($\chi^2(2, N = 16) = 2.33$, $p = 0.31$, $\eta^2 = .16$) (see Figure 12).

**Figure 12.** Comparison of the total duration of time that each dolphin spent at the window in both the baseline and control conditions. There was no significant difference between the amounts of time each dolphin spent at the window in either the baseline or control conditions.
Mark test sessions

A total of 18 mark tests were conducted (9 Foster, 3 Bayley, 6 Nani); for four of the mark test sessions there was a malfunction with the marker (the ink did not adhere to the dolphins’ skin), but these sessions were still analyzed because they are comparable to the late sham marks done in the Reiss & Marino (2001) study (see Table 3). All three of the dolphins passed the mark test at least once during this study.

Table 3

Date of mark/control sham mark test sessions, age at mark test, location of mark/control sham mark, and mark test results for each dolphin.

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<td></td>
<td>11/16/11</td>
<td>3</td>
<td>2 Mark between pectoral fins</td>
<td>Passed</td>
</tr>
<tr>
<td>Nani</td>
<td>06/04/09</td>
<td>37</td>
<td>0 Mark right side of head,</td>
<td>Ambiguous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Control Sham left side of head</td>
<td></td>
</tr>
<tr>
<td></td>
<td>06/06/09</td>
<td>37</td>
<td>0 Mark between pectoral fins, *</td>
<td>Passed</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Control Sham above pec, lateral</td>
<td></td>
</tr>
<tr>
<td></td>
<td>06/10/09</td>
<td>37</td>
<td>0 Mark between pectoral fins</td>
<td>Passed</td>
</tr>
<tr>
<td></td>
<td>06/12/09</td>
<td>37</td>
<td>0 Mark between pectoral fins (lower)</td>
<td>Passed</td>
</tr>
<tr>
<td></td>
<td>10/12/11</td>
<td>39</td>
<td>0 Mark between pectoral fins</td>
<td>Did not pass</td>
</tr>
<tr>
<td></td>
<td>12/07/11</td>
<td>39</td>
<td>0 Mark between pectoral fins</td>
<td>Did not pass</td>
</tr>
</tbody>
</table>

Note: Lines denoted with a * indicate days when there was a malfunction with the marker.
Out of a total of 3 mark test sessions, Bayley passed the first mark test. During this session, after being marked between her pectoral fins, Bayley (aged 2-years, 7-months) exhibited ventral orientations with repetitive head and body movements in the vertical plane and she repeatedly stretched her neck up. During the same session, prior to being marked, Bayley did not exhibit any repetitive head and body movements in the vertical plane. Bayley spent more time at the mirror after (167 seconds) being marked than she did before she was marked (103 seconds) and she was alone at the mirror most of the time (pre: $f = 23$, 95.8%; post: $f = 26$, 81.3%).

The second mark test session with Bayley was scored as ambiguous, but not because of a lack of mark-directed behaviors. Following being marked on the right side of her head, Bayley oriented to the right side of her head ($f = 9$) and moved her head down; however, when looking at her behavior in the mirror prior to being marked she oriented to the right side of her head an equal number of times ($f = 9$). However, after being marked Bayley exhibited more left orientations ($f = 7$) than prior to being marked ($f = 1$), which may suggest that she was investigating both sides of her head and making comparisons. It is important to note that when all of Bayley’s behaviors from the 3 mark tests were combined ($f = 120$) there appeared to be a slight preference for orienting to the right ($f = 26$, 21.7%) versus the left ($f = 13$, 10.8%). During this second session, Bayley was alone at the mirror more frequently prior to being marked ($f = 28$, 90.2%) and 100% of the time after she was marked. Bayley did not pass the last mark test because she never stationed at the mirror following being marked. During this session Bayley did not show much interest in the mirror prior to being marked either. Bayley spent more time at the mirror after being marked for only the one mark test that she passed.

Out of a total of 9 mark test sessions, Foster passed five mark tests. It is important to note that when all of Foster’s behaviors from the 9 mark tests were combined ($f = 888$) there appeared
to be a preference for orienting to the right ($f = 138, 16.4\%$) versus the left ($f = 44, 5.2\%$).

Foster’s first mark test was scored as passing even though he did not orient his body or his head to the left as often as expected because he was marked on the left side of his head above the eye. He showed more orienting to the right ($f = 35, 40.2\%$) versus the left ($f = 6, 6.9\%$) after being marked. However, after being marked, Foster exhibited stereotyped behavior that was different from the behavior observed before he was marked. He continually stationed at the edge of the mirror with the left side of his body in view and he repeatedly tilted his body and head to the right. This appeared to expose the left side of his head and the mark to more light. These behaviors occurred in 10 out of the 14 bouts where Foster approached the mirror after being marked. There was only one brief instance of this behavior, out of the 21 bouts where Foster approached the mirror prior to being marked. Prior to being marked, Foster was alone at the mirror a little more than half of the bouts ($f = 80, 53.7\%$), while after being marked he was alone more often ($f = 78, 89.7\%$).

The second mark test for Foster was scored as ambiguous. Foster was marked between the pectoral fins, but the marker malfunctioned (the ink did not adhere to his skin) and instead of an “X” there was a partial mark (a diagonal line). Foster exhibited compelling self-directed behavior during this session prior to being marked and he spent more time at the mirror (416 seconds). After he was marked, Foster only spent a total of 127 seconds at the mirror. Notably, within 9 seconds of being marked Foster swam by the mirror with the mark visible and glanced at the mirror (very briefly) and he first stationed at the mirror only 17 seconds after being marked. This behavior suggests that he may have been motivated to look for a mark; however, since the mark (a partial line) was unclear, it may have resembled a typical rake mark and may not have appeared salient. As a result, Foster may have lost interest in investigating the marked
location further. Foster was alone at the mirror more often both pre ($f = 56, 70\%$) and post ($f = 23, 88.5\%$) being marked.

Foster’s third mark test session was conservatively scored as ambiguous because he exhibited similar behaviors before and after being marked. Prior to being marked Foster started exhibiting a new behavior called “airplane” (AP, $f = 2$) where he stretched his neck up and positioned his pectoral fins perpendicular to his body. He also stretched his neck up ($f = 5$) and stationed at the mirror with a ventral orientation. These are all types of behaviors you would expect to see if Foster was marked between his pectoral fins; however, he had not been marked yet. After being marked between his pectoral fins Foster exhibited similar behaviors: he produced AP ($f = 3$), stretched his neck up ($f = 7$), and stationed with ventral orientations. He also repeatedly somersaulted ($f = 3$) in the horizontal plane and paused between each somersault, with his ventral surface facing the mirror, and appeared to look in. Typically, swim-bys are not coded unless they last for more than 3 seconds; however, it is interesting to note that on eight different occasions, Foster swam close by the mirror with his ventral surface facing the mirror. Foster was alone at the mirror both pre and post being marked, 98% of the time.

The fourth mark test session for Foster was scored as not passing because there was very little compelling mark-directed orientation and behavior, apart from the very end of the session when the mirror was about to be removed. At that time, it was possible that Foster heard movement in the pit and stationed at the mirror, so this segment was not used to prevent having false positive results. Interestingly, Foster did swim directly towards the mirror immediately following being marked (within 7 seconds); however, he did not station and instead swam by with the marked side of his head toward the mirror. Foster did not pass the fifth mark test
(1/22/10) because he never stationed at the mirror following being marked. Foster showed very little interest in the mirror prior to being marked as well.

Foster successfully passed the last four mark tests. When conducting the sixth mark test with Foster, the mark was supposed to be between his pectoral fins; however, after multiple failed attempts with two different markers the trainers stopped trying to mark him. Even though Foster spent more time at the mirror (125 seconds) and exhibited more behaviors ($f = 24$) prior to being marked versus after being marked (53 seconds, $f = 11$), this session was still scored as passing. Foster exhibited compelling mark-directed behaviors even though a mark did not show up: he stationed inverted and head on with his ventral surface showing, on two separate occasions he oriented with his ventral surface facing and touching the mirror (BSW). This behavior suggests that Foster could feel that he had been marked; however, it appears that after investigating the marked area and not seeing a mark, his interest in observing that area decreased. Foster was alone at the mirror 100% of the time, both pre and post being marked.

During the seventh mark test session with Foster there was a malfunction with the marker (the ink did not adhere to his skin). The mark was supposed to be on the inside of one of his pectoral fins, but instead there were partial marks (a few faint straight lines) on the inside of both of his pectoral fins. During analysis of the video from this session I could not see a mark on Foster, but close-up above water video after the session confirmed the presence of these marks. Even though Foster most likely could not see the partial marks, he would have felt that he was marked and he oriented his body in ways that would allow for investigation underneath his pectoral fins. Foster exhibited BSW ($f = 5$), he stretched his neck up and arched his body, and he repeatedly tilted his ventrally oriented body to the left, in order to look at the under side of his pectoral fins. These behaviors were absent prior to him being marked with the exception of one
instance of him stretching his neck up. As a result, this mark test session was scored as a pass.

Foster spent less time at the mirror before being marked (203 seconds) versus after being marked (246 seconds). Also, prior to being marked, Foster was with Bayley \(f = 18, 66.7\%\) at the mirror more often than he was alone \(f = 9, 33.3\%\), but after being marked this changed and Foster was alone \(f = 31, 83.8\%\) most of the time.

For the eighth mark test session Foster was marked between his pectoral fins and he exhibited mark-directed behaviors. For example, Foster oriented his ventral surface to the mirror and repeatedly titled his body to the left and right (number of bouts, \(f = 6\)) and he repeatedly moved his head up and down (number of bouts, \(f = 4\)). He also spent more time at the mirror after being marked (196 seconds) than he did prior to being marked (23 seconds) and he was alone at the mirror 100% of the time both before and after being marked.

During the last mark test session Foster appeared to be highly motivated to investigate the mark (between pectoral fins towards left) because he swam directly to the mirror within 5 seconds of being released by the trainers after being marked. The mark-directed behaviors that Foster exhibited during this session were the most compelling of all sessions. He repeatedly oriented his ventral surface to the mirror, arched and titled his body so that he was almost inverted, and lifted his pectoral fins. Although the mark was between his pectoral fins, it was a little to the left, which explains why Foster continually tilted towards his right, causing the left side of his ventral surface to be more exposed. Foster exhibited compelling self-directed behavior throughout this entire session (both pre and post mark) and he spent more time at the mirror prior to being marked (859 seconds) than he did after he was marked (156 seconds). Prior to being marked Foster was with Beau \(f = 81, 55.9\%\) at the mirror, more than he was alone \(f = 64, 44.1\%\). However, after he was marked Foster was alone at the mirror 92% of the time.
Out of a total of 6 mark test sessions, Nani passed three of the mark tests. Overall, when all of Nani’s behaviors from the 6 mark tests were combined \( f = 227 \) there did not appear to be a preference for orienting to the right \( f = 44, 19.4\% \) versus the left \( f = 40, 17.6\% \). For Nani’s first two mark test sessions, she was marked on one side of her head and also control sham marked on the opposite side of her head. In the first mark test with Nani (marked on the right side of her head & sham marked on the left side of her head), she exhibited mark-directed behavior, but to be conservative, the test was scored as ambiguous because her mark-directed behaviors were brief and she exhibited right orientations prior to being marked as well. It is important to note that on this day, after being marked and sham marked, when Nani first came to the mirror she oriented her head to the right (the marked side) and then to the left (the sham marked side). Also, even though she showed right orientations prior to being marked \( f = 6 \), she did orient more to the right after being marked \( f = 11 \). Nani was with Beau at the mirror more frequently both before \( f = 18, 60\% \) and after \( f = 23, 92\% \) being marked than she did alone.

When conducting the second mark test with Nani, the trainers attempted repeatedly to mark her with the marker between her pectoral fins; however, the marker malfunctioned (the ink did not adhere to her skin) and after several attempts the trainers stopped marking her. She was also given a control sham mark above her pectoral fin on the lateral side of her body. This mark test was scored as a pass even though no mark was visible between her pectoral fins because Nani engaged in multiple ventral orientations, was clearly lifting her head up, and splaying her pectoral fins out to the side. It is not surprising that Nani did not appear to be looking for a mark where the trainers did the control sham because they did not spend as much time marking that area as they did when trying to mark her between her pectoral fins. Overall Nani appeared motivated to look at the area between her pectoral fins. In fact, she spent more time at the mirror
after being marked (201 seconds) versus prior to being marked (94 seconds). Nani was with Beau ($f = 10, 52.6\%$) at the mirror more often than she was alone prior to being marked and she was alone ($f = 28, 60.9\%$) more often after being marked.

The third mark test with Nani was scored as passing. Nani appeared motivated to investigate the mark (between her pectoral fins) because she came to the mirror within 9 seconds of being marked; however, she only remained at the mirror for a brief (6 seconds) time. She also spent more time at the mirror after (168 seconds) being marked than before (69 seconds) she was marked. Nani exhibited more ventral orientations at the mirror after she was marked and she repeatedly arched and rocked her body back exposing her ventral surface. During one compelling bout of mark-directed investigation, Nani oriented her body horizontally with her ventral surface and her head facing the mirror and she remained in this position for 5 seconds. Nani was alone at the mirror a comparable percentage of time before ($f = 14, 87.5\%$) and after ($f = 28, 77.8\%$) being marked.

The fourth mark test with Nani was scored as passing because she appeared highly motivated to investigate the marked area (between her pectoral fins). She stationed at the mirror 18 seconds after being marked, and she exhibited very compelling mark-directed behaviors at the mirror. Nani exhibited multiple ventral orientations, was clearly lifting her head, and was moving her body in both the vertical and horizontal planes, exposing her ventral surface and the mark. During this session Nani was with other dolphins at the mirror more often both pre ($f = 10, 52.6\%$) and post ($f = 17, 54.8\%$) being marked. Nani did not pass the last two mark tests because she never stationed at the mirror following being marked. During both of these sessions there was a lot of social activity between the dolphins in the pool, which may have impacted her
motivation to station at the mirror. Notably, Nani spent more time at the mirror after being marked for all of the mark-test sessions that she passed.

The overall duration of time spent at the mirror before and after being marked was calculated by combining the durations across sessions for each dolphin. Wilcoxon Signed-Rank tests were conducted to determine if Bayley, Foster, and Nani spent more time at the mirror after being marked versus before they were marked. Results demonstrated that for all three dolphins there was no significant difference between the median duration of time spent at the mirror after being marked and the median duration of time spent at the mirror before they were marked; Bayley ($Z = 0.54, p = 0.14$), Foster ($Z = 1.58, p = 0.11$), and Nani ($Z = 1.46, p = 0.14$).


Discussion

The main goals of this developmental study were to 1) further confirm the capability of MSR in bottlenose dolphins, 2) determine the age of emergence of MSR in this species, 3) give a more in depth description of the stages of behavior and specific mirror-mediated behaviors exhibited throughout mirror exposure by each dolphin, and 4) draw comparisons with data documenting the emergence of this ability in humans and great ape species. In the following sections I discuss the main findings regarding the development of MSR in bottlenose dolphins, discuss critical issues when conducting MSR research, and also suggest future avenues of research.

Confirmation of MSR in dolphins

The results from this study supported the initial prediction that these dolphins would demonstrate MSR, a further confirmation of this ability in this species. Not only did all three of the dolphins successfully pass the mark test, but they also exhibited predominately self-directed behavior when at the mirror and did so after minimal mirror exposure. Results also supported the prediction that MSR emerges in dolphins at an age comparable to humans and chimpanzees.

Mark tests. Out of a total of 3 mark test sessions, Bayley only passed the first mark test at the age of 2-years, 7-months. When marked for the first time (between the pectoral fins) Bayley exhibited mark-directed behaviors (ventral orientations, repetitive head & body movements in the vertical plane & repeated neck stretches) that were not observed during that session prior to being marked. Notably, during this session when Bayley returned to the mirror, after already showing mark-directed behaviors, the mark was smeared; however, because the researchers did not observe Bayley rubbing her ventral surface, it could not be determined if this was done intentionally in an attempt to remove the mark. Even though her second mark test was
scored as ambiguous, Bayley (marked on the right side of head) exhibited mark-directed behavior (oriented her head to the right and left & moved her head down). Because she also oriented her head to the right an equal number of times prior to being marked it was difficult to confirm that she was investigating the mark, even though her post-mark behavior suggested that she may have been comparing the marked and unmarked sides of her head.

Out of a total of 9 mark test sessions, Foster passed five mark tests. Foster passed the first mark test (aged 2-years, 2-months) and he exhibited compelling stereotyped mark-directed behavior. Foster’s next passing mark test was when he was 2-years, 9-months (sixth mark test session). During this session, Foster exhibited compelling mark-directed behaviors even though no mark was present (ink did not adhere to his skin). He stationed inverted and head on with his ventral surface showing and on two separate occasions he oriented with his ventral surface facing and touching the mirror (BSW). This behavior suggests that Foster could feel that he had been marked; however, it appears that after investigating the marked area and not seeing a mark, his interest in observing that area decreased. These behaviors are synonymous to the types of behaviors observed in a previous dolphin MSR study when a dolphin was sham marked after he had experienced being marked with a visible mark (Reiss & Marino, 2001).

Foster’s behavior during 2 subsequent passing mark test sessions, in which he passed the mark test, was very similar to the behaviors that were previously seen being exhibited by Presley, a dolphin from previous MSR tests with dolphins (Reiss & Marino, 2001). Foster exhibited somersaults in the horizontal plane, repeated ventral orientations and lifted up his pectoral fins in order to investigate marks between and underneath the pectoral fins. During his last mark test session, Foster appeared highly motivated to investigate the mark (between pectoral fins) because he swam directly to the mirror only 5 seconds after being marked and he
exhibited some of his most compelling mark-directed behaviors. He repeatedly oriented his ventral surface to the mirror, arched and titled his body so that he was almost inverted, and lifted his pectoral fins. Notably, the fourth time Foster stationed at the mirror during this session, less than 5-minutes after being marked, the mark between his pectoral fins had been smeared. As with Bayley, the researchers did not observe Foster rubbing his ventral surface, so it could not be determined if this was an intentional attempt to remove the mark. This behavior has been seen previously; an early inconclusive MSR study with dolphins reported that one of the dolphins attempted to remove a zinc oxide mark by rubbing against the tank wall (Marten & Psarakos, 1995).

Nani (37-years of age) passed three out of six mark tests. Nani’s first mark test was scored as ambiguous even though she was demonstrating mark-directed behavior because her behavior was brief and she exhibited similar behavior prior to being marked. Similar to Foster, Nani passed her second mark test even though no mark was present (ink would not adhere to her skin) between her pectoral fins because she exhibited mark-directed behaviors and appeared motivated to look for a mark where the trainers had made multiple attempts at applying one. She engaged in multiple ventral orientations, was clearly lifting her head up, and splaying her pectoral fins out to the side. Nani (marked between her pectoral fins) passed her next two mark test sessions because she exhibited compelling mark-directed behaviors (lifted her head, repeatedly arched, rocked and moved her body in both horizontal and vertical planes exposing her ventral surface) and she appeared to be highly motivated to investigate the mark. During both of these sessions she exhibited a shorter latency (< 20 seconds) to station at the mirror following being marked, which was not typical for these dolphins.
Unlike dolphins in Reiss and Marino’s (2001) MSR study, dolphins in this study tended to demonstrate delayed orientation at the mirror following being marked. The dolphins showed evidence for looking at the mark, but they did not always swim directly to the mirror to investigate the mark. Of the 18 mark test sessions, Nani and Foster demonstrated a shorter latency (less than 20 seconds) to station at the mirror in only 4 sessions (2 sessions for Nani, 2 sessions for Foster). In one additional mark test session, Foster swam directly to the mirror within 7-seconds of being marked, but he did not station and instead just swam by. A difference in the handling of the dolphins by the trainers may have contributed to this distinction between the current study and Reiss & Marino’s (2001).

As reported in previous MSR studies with chimpanzees (Gallup, 1970; Povinelli et al., 1993), both Nani and Bayley tended to spend more time at the mirror after being marked than they did prior to being marked; however, this difference only applied to mark test sessions that were scored as passing. A comparison of the total duration of time across all sessions that each dolphin spent at the mirror before and after being marked showed that no difference existed. Therefore, overall duration of time spent at the mirror before and after being marked may not always be a useful indicator in determining whether or not the individual has passed the mark test. For example, Foster spent more time at the mirror after being marked for only 3 of the 9 mark test sessions and only 2 of these were mark tests that he passed. The fact that the mark was not visible, it did not adhere to the dolphin’s skin, for 3 of the mark test sessions may have also contributed to this finding.

During Foster’s last mark test session he passed the mark test and exhibited some of his most compelling mark-directed behaviors; however, he spent considerably more time at the mirror prior to being marked and he exhibited compelling self-directed behavior throughout the
entire session (both pre and post mark). This difference may be explained by a reorganization of the dolphin subgroups. Towards the end of this study, in the fall of 2011, Beau and Foster were permanently separated from the female dolphins. As a result, this session was only the second time that Foster had seen the mirror in almost 8 months (he had mirror exposure the week prior) and Foster and Beau were the only dolphins in the pool. This situation may have contributed to Foster’s increased motivation to view himself at the mirror.

The use of previous mark tests with dolphins has been questioned, “because of their lack of hands, the dependent variable was not reaching for the mark as required in the standard task (Suddendorf & Butler, 2013, p. 122)”. It is conceivable that the dolphins in this study were interested in investigating the mark that they saw in the mirror, but thought that it was on another dolphin. However, this conclusion is unlikely because if these dolphins were interested in looking at the “other marked dolphin in the mirror” they would only need to station at the mirror to see it, but instead they position themselves close to the mirror and contort their body in ways that allows them to investigate the mark on their own body. Also, the dolphins in this study and the previous study by Reiss and Marino (2001) did not appear to show an interest towards the marks that were on other dolphins in their same pool. This is not surprising because dolphins are not social or self-groomers and their bodies often have new and old rake marks, marks made by the dolphins running their teeth over the skin of another in social interactions.

**Early onset of self-directed behavior at the mirror**

Notably, in the current study, self-directed behavior was observed at an earlier age in dolphins (5 ½ months & 14 ½ months) than reported for humans (18-24 months) and chimpanzees (28-30 months & 4.5 years). Bayley, the youngest dolphin was observed demonstrating self-directed behavior (e.g. close eye viewing, bubble production, & stretching
neck up) at the mirror on her fourth day of mirror exposure, at 5 ½ months of age. Foster demonstrated self-directed behavior (e.g. close eye viewing, open mouth viewing, & bubble production/play) on his first day of mirror exposure at the age of 14 ½-months. The early onset of self-directed behavior may be due in part to the fact that dolphins are precocious at birth exceeding human and non-human primates in motor skills and coordination. In a long-term field study of the development of wild bottlenose dolphin calves, observations demonstrated that during the first week post-partum, calves continued to locomote and only rested a few seconds at a time (Mann & Smuts, 1999). Unlike humans and other primates, dolphin calves must be able to nurse while swimming with their mothers. Therefore, during their first week of life, most dolphin calves have developed high levels of synchronized swimming and breathing with their mothers (Mann & Smuts, 1999). Dolphin calves in the wild also experience brief periods of separation from their mothers when the mothers are foraging; this fact makes recognizing their mothers imperative for successfully reuniting with them. Mann & Smuts (1999) suggest “Integration of complex sensorimotor tasks seems especially critical for newborn mammals in a marine environment (p. 562).” The inherent demands of being a highly social species living in an aquatic environment may be partially contributing to the early onset of MSR.

Due to the highly complex fission-fusion type of organization of dolphin societies, their social and cognitive skills are also developing at a young age. Dolphins, unlike humans and other primates, are not clinging to their mothers when they are young. As a result, they have more opportunities for engaging with other members of their social group at a much younger age. In fact, dolphins engage in social play behaviors with individuals other than their mothers within the first week of life (Mackey, Makecha, & Kuczaj, 2014; Mann & Smuts, 1999) and within the first 2 weeks, male calves are even engaging in sociosexual behavior (i.e. rubbing) (Mann &
Having to negotiate social relationships at such a young age requires that young dolphins would develop an understanding and awareness of self and others. Therefore, it should not be surprising that Bayley was showing self-directed behavior at such a young age.

**Stages of behavior and specific mirror-mediated behaviors**

**Social Behavior.** For all of the dolphins in this study, almost no social behavior was observed on the first day of mirror exposure, which was expected because these dolphins were not naïve to reflective surfaces. The only dolphin to exhibit social behavior on the first day of mirror exposure was Foster (2 whistle bubble streams & 2 instances of echolocation); however, the fact that much of his behavior on that same day was self-directed suggests that he may have had sufficient experience with mirror reflections and recognized his image in the mirror and those 4 behaviors could be considered self-directed social. Also, since these dolphins were in social groups throughout the mirror study, instances of whistle bubble streams, in the absence of other social behaviors at the mirror, can be considered ambiguous. It is difficult to discern if this behavior was directed at the dolphin’s reflection or if it was a communicative response directed at another dolphin in the pool.

Bayley first showed what appeared to be social behavior (squawking & whistle bubble stream) at the mirror on her 16th day of mirror exposure (6/5/09) when she was a little over 10-months old; months after she began showing self-directed behavior. As I will discuss in more detail later, these “social” behaviors may have been an example of deferred imitation by Bayley. Nani first showed social behavior (e.g. 2 head jerks) on her third day of mirror exposure, after she had already been exhibiting self-directed behavior. Nani’s highest frequency of “social” behaviors was on her 10th day of mirror exposure (6/3/09) and involved mostly echolocation, two whistle bubble streams and head jerking. On June 3rd through June 5th there appeared to be
extensive social interactions between the dolphins in the pool, which may have contributed to the increase in “social” behavior exhibited at the mirror. A more detailed discussion regarding whether or not these delayed “social” behaviors should be categorized as social, is addressed later in the discussion under the contextual categories of mirror-directed behaviors heading.

**Contingency-testing (CT).** Bayley first exhibited contingency-testing behaviors (head & body movements) on her fourth day of mirror exposure (the same day she started exhibiting self-directed behaviors), but they were infrequent ($f = 3$) and then disappeared. Repetitive behaviors exhibited by Bayley were not observed again for over 2 months. This supports previous studies with chimpanzees that reported seeing a rapid transition from contingent body movements to self-exploratory behaviors in some individuals (Povinelli et al., 1993). The boundary between contingency-testing and self-directed behaviors is often unclear because CT can be fleeting, which makes determining the emergence of these behaviors sometimes difficult. This may explain the discrepancies seen in the human (Dixon, 1957; Amsterdam, 1972) and great ape (Robert, 1986; Povinelli et al., 1993) literature regarding the age of emergence for CT behaviors.

If the individual being tested for MSR is already demonstrating compelling self-directed behavior when first exposed to the mirror then CT behaviors may be absent all together and any repetitive behaviors exhibited are most likely self-directed. This is what is seen in the current study with both Foster and Nani. However, due to Foster’s young age, to be conservative, any repetitive behaviors he exhibited in the first month of mirror exposure were still categorized as CT. Nani exhibited repetitive behaviors in all but three of the mirror sessions; however, since she demonstrated self-directed behavior in the absence of social behavior on day one, only instances of repetitive behaviors exhibited on this day were conservatively categorized as CT.

**Specific mirror-mediated behaviors.** The dolphins did not usually vocalize during these
bouts or in early sessions when first exposed to the mirror, which suggests they were not reacting socially. The dolphins in this study demonstrated specific behaviors similar to those described in previous research conducted with dolphins (Marino, Gallup, & Reiss, 1994; Marten & Psarakos, 1994, 1995; Reiss & Marino, 2001; Sarko et al., 2002), humans (Amsterdam, 1972; Bard et al., 2006; Dixon, 1957), and chimpanzees (Bard et al., 2006; Gallup, 1970; Povinelli et al., 1993). Despite differences in morphology, humans, chimpanzees, and dolphins (including those in this study) have all exhibited the following behaviors: open mouth viewing (tongue movements), close eye viewing, horizontal and vertical head and body movements, flexing and contorting body (described in chimpanzees and dolphins) moving extremities (e.g. fins or arms) up and down, watching themselves blow bubbles at the mirror, vocalizing (different types depending on species), and they have even interacted with others and used the mirror as a tool to monitor these interactions.

When looking at the individual behaviors exhibited by the 3 dolphins in this study, there were a few behaviors that seemed to differ from those reported in other dolphins (Reiss & Marino, 2001). For example, Foster exhibited a specific behavior, body splay window (BSW) where he would swim up to the mirror and in one continuous motion slide the ventral surface of his body across the window with his pectoral fins perpendicular to his body and his neck stretched up. This behavior was never exhibited by Nani and was observed only twice for Bayley, while Foster engaged in this behavior more frequently ($f = 106$). It is possible that this behavior made it easier for Foster to view his own erection at the mirror since he was observed on a few occasions having an erection while simultaneously performing this behavior. One could also argue that this behavior was arousing because it involved rubbing his ventral surface, including the genital region, on the window. Foster also exhibited more head jerks (HJ, $f = 178$)
and squawking \((YW, f = 385)\) in front of the mirror more than Bayley and Nani. In fact, these behaviors comprised the majority of his self-directed social behaviors. It is possible that these behaviors could be due to sex differences, but could also be due to playfulness in younger dolphins and or imitative behaviors because Bayley started to exhibit some of these behaviors after observing Foster. Additional research with various aged dolphins of both sexes would be needed to make these and other behavioral comparisons between males and females.

Notably, some of the most frequent behaviors exhibited by the dolphins in this study were conservatively categorized as ambiguous. For example, head butting the mirror and making contact with the mirror using the rostrum were both in the top three most frequent behaviors. The function of these two behaviors is unclear, but it is possible that they provided both tactile and auditory feedback for the dolphins. The dolphins in this study did not just touch the mirror with their rostrum; they would also drag their rostrum across the mirror creating a squeaking sound. It is also possible that the tactile and auditory aspects of these behaviors were some how reinforcing. Both of these behaviors simultaneously occurred with bouts of self-directed behaviors and were then categorized as self-directed. Head butting occurred in contexts of both social and solitary play at the mirror. For example, Foster was observed head butting the mirror while in synchronous dyadic interactions with several different dolphins (Bayley, Beau, & Jade). During one compelling interaction, prior to Foster being marked, Beau (not analyzed for this thesis) and Foster engaged in repeated bouts of taking turns head butting the mirror and during one of these bouts the behavior repeated 14 times. Synchronized behaviors at the mirror have also been reported in previous MSR studies with dolphins (Marino et al., 1994)

**Turn taking and synchronous behavior at the mirror: Play**

Some of the most compelling, repeated, and long lasting behaviors produced by the
dolphins in the current study involved play (both social and solitary). Dolphins engage in play throughout their entire life and it has been suggested that of all mammal species, dolphins and other marine mammals may be the most playful (Fagen, 1981, as cited in Burghardt, 2005 p. 154). The previously discussed turn taking and synchronous behaviors exhibited at the mirror may be considered a form of social play and the mirror itself an object of this play interaction or a tool used to investigate what these play activities look like. As I previously mentioned, social play is exhibited within a bottlenose dolphin’s first week of life (Mackey et al., 2014; Tizzi et al., 2000). Social play is an important aspect of the development of young dolphins’ social cognitive skills because it assists them in learning the appropriate behaviors needed for engaging in successful interactions with conspecifics (Mackey et al., 2014). Some forms of social play exhibited by both wild and captive dolphins that involve turn taking and synchronous acts include: sociosexual play, reciprocal chasing, & mimicking others’ play behaviors (both novel and familiar) (Mackey et al., 2014). Turn taking and other forms of synchronous play behavior at the mirror (e.g. repeated circling and head butting) between Foster and Beau may be important in strengthening the bond between two male dolphins that, in the wild, would most likely forge a life-long relationship or alliance (Herman, 2012; Mackey et al., 2014). According to developmental research with children, the age of emergence of synchronous imitation (behavioral mimicry), pretend play, and mirror-self recognition are all associated, and most children develop these abilities by the age of 2 (Herman, 2012; Nielsen & Dissanayake, 2004). It is then parsimonious to conclude that dolphins demonstrating MSR should also have the capacity for synchronous imitation and pretend play.

**Mirror-directed bubble behavior: Play**

Previous MSR studies have yet to conduct a detailed analysis of mirror-directed bubble
behaviors; however, several studies have previously described and quantified dolphin bubble play behavior (Kuczaj et al., 2006; Marten et al., 1996; McCowan et al., 2000; Pace, 2000; Paulos et al., 2010). In the current study, bubble production included some of the most frequently occurring behavior for all three dolphins; as a result, the first detailed analysis of mirror-directed bubble behavior was conducted. Results concluded that mirror-mediated bubble behaviors in dolphins were exhibited in multiple contexts (solitary & with others, calm & aroused, from the blowhole or mouth) and were expressed across a spectrum of complexity (see Appendix B). Foster produced the highest number of bubble behavior events and he was the only dolphin to produce all 18 variations of the observed bubble behavior events. I hypothesize that much of the mirror-mediated bubble behavior observed in this study can be considered solitary/object play because most bubble behaviors occurred when the dolphins were alone at the mirror. One of the most complex and compelling mirror-mediated bubble behavior events was the “inverted smash bubble”. During this behavior the dolphin (almost always Foster) would produce a bubble burst or multiple bubbles and proceed to smash the bubbles with their head or rostrum (sometimes biting the bubbles) creating a cloud of bubbles, all while in an inverted position. This is not a behavior that is typically observed in these dolphins in the absence of the mirror.

Notably, the dolphins in this study have also been observed exhibiting other forms of innovative bubble play, in the absence of the mirror. For example, Bayley (the youngest dolphin) has been observed creating bubble rings with both her blowhole and her fluke. For several months throughout this study, when Bayley was about 2-years old, she began producing a cloud of bubbles from her blowhole that she would swim through and then use her fluke to create a bubble ring. She then proceeded to play with the bubble and was even observed once to use her blowhole to create a second bubble ring inside the ring she had just created with her fluke.
Bayley engaged in this fluke bubble ring behavior repeatedly, sometimes for as long as an hour, which is a considerable amount of concentration for such a young animal. The coordination, concentration, and anticipatory behavior involved in this type of solitary play is further evidence for the precocious motor and cognitive development seen in dolphins and supports the current findings showing that Bayley demonstrated self-directed behavior at such a young age.

**Duration of time spent at the mirror**

Results demonstrated that all three dolphins spent more time at the mirror in the experimental conditions versus at the window in both the baseline and control sessions. Even though some reflectivity existed in the windows during the baseline and control sessions, stationing was still infrequent. As with previous MSR studies with dolphins (Marino et al., 1994; Reiss & Marino, 2001; Sarko et al, 2002), we did not see the duration of time spent at the mirror decrease over sessions, which contradicts results from MSR studies with chimpanzees. Both Gallup (1970) and Povinelli et al. (1993) reported that the chimpanzees habituated to the mirror. The dolphins in this study did not appear to habituate to the mirror, which may be explained by the amount of mirror exposure they were given during each session. The dolphins were given access to the mirror for a maximum of 1 hour, up to twice a week. This is different from studies with chimpanzees where the animals had access to the mirror for up to 8 hours per day, several days in a row (Gallup, 1970; Povinelli et al., 1993). Findings from this study also contradict previous research with chimpanzees that has shown older individuals lose interest in the mirror (de Veer et al., 2002; Povinelli et al., 1993). Nani, the oldest dolphin (37-39 years), had less access to the mirror and yet spent more time at the mirror than Bayley (the youngest dolphin). The frequency of stationing at the mirror is also important because, just as with duration of time spent at the mirror, it suggests dolphins’ motivation to investigate reflections in the mirror. An
increase in stationing at the mirror also offers more opportunities for social learning by watching others engage at the mirror.

Foster spent more time at the mirror than both Nani and Bayley combined and he produced more behaviors at the mirror (even after controlling for differences in amount of mirror exposure), which might be due to his unique history. Foster, as his name implies, did not have the opportunity to bond with his mother Jade. At an early age Foster was taken from his mother Jade by another dominant female in the pool, Shiloh, and it is unclear if this occurred because his mother was neglecting him. As a result, Foster did not have a strong maternal bond and he developed independence from his female caretakers at an early age. This may have contributed to Foster’s increased time spent at the mirror and engagement in mirror-oriented behaviors and may explain why three-quarters of his behaviors were exhibited while he was alone at the mirror.

**Contextual categories of mirror-directed behaviors**

An important consideration and contribution of this study is how the dolphins’ behaviors at the mirror were categorized. Initially, behaviors were categorized using the three behavioral stages (i.e. social, contingency-testing, & self-directed) that have been documented in all species previously shown to be capable of MSR. However, in some sessions after the dolphins were reliably exhibiting compelling self-directed behavior, they began to exhibit what appeared to be social behaviors (e.g. squawking, head jerks, & jaw claps). Also, throughout mirror exposure, the dolphins produced repetitive behaviors while simultaneously producing bouts of self-directed behaviors. Such behavior might generally be interpreted as a dolphin reverting back to the prior two stages (social & contingency-testing); however, this explanation seems highly unlikely and is unparsimonious. Instead I hypothesize that these “social” and “contingency-testing” behaviors are self-directed in nature based on the behavioral context in which they occur. It is important to
consider the overall context, specifically the individual’s previous history of mirror exposure, the types of behaviors and mirror-directed behaviors previously produced, and the coinciding behaviors observed during the same session. Without considering the overall trajectory of the individual’s behavioral responses at the mirror in the course of mirror exposure over the study, the intricacies and nuances of each individual’s emerging behavior at the mirror may be misinterpreted or categorized erroneously. In this study, the original categories were reevaluated and contextual categories were added that were termed *repetitive self-directed, self-directed social, and repetitive self-directed social*.

These additional categories represent behavior in context and provide a more detailed picture of how the dolphins’ overall behaviors developed throughout mirror exposure. With continued mirror exposure, it appears that the dolphins in this study and other animals develop a curiosity about what their reflection looks like when they are engaging in a variety of behaviors and they use the mirror as a tool to make these observations. As I previously discussed, these behaviors may also be forms of pretend play or even role-playing at the mirror. Previous studies with dolphins have shown that their play interactions (both social and solitary) become more complex throughout development (Kuczaj et al., 2006; Mackey et al., 2014), which was observed in Foster’s behavior and was beginning to be seen in Bayley’s behavior. As previously mentioned, the first time Foster squawked while at the mirror was on 6/3/09. During this time he was also exhibiting other *self-directed social* behaviors, such as head jerks, he was simultaneously producing bubbles, and often had a wide-open mouth displayed. This series of behaviors increased in complexity as Foster started to barrel roll, repeatedly move his head and body from side-to-side, and even become inverted, all while producing these behaviors. One interpretation of these late occurrences of “social” behaviors being embedded within the context
of self-directed behaviors is that Foster may have been practicing some of the motor behaviors needed later in life during aggressive interactions by engaging in solitary play in front of the mirror (Burghardt, 2005; Mackey et al., 2014). Solitary play involving head jerks and jaw claps has even been observed in wild dolphin calves as young as 3-4 weeks of age (Mann & Smuts, 1999). According to Mann and Smuts (1999), these “social” behaviors were considered solitary play because they were exhibited when the calves were alone (< 10m from others). It is also possible that these calves were imitating behaviors they had previously observed other dolphins exhibiting.

**Self-directed social behavior: Social learning and imitation**

I observed that certain behaviors that were exhibited at the mirror by one animal were exhibited a short period of time later by another animal in the same social group. For example, two days after Foster started to exhibit the complex sequence of self-directed social behavior described in the paragraph above, Bayley was observed squawking, bubbling, and opening her mouth wide. She had been in the pool with Foster during the previous two sessions in which he repeatedly exhibited squawking, head jerks, bubbling, and wide-open mouth displays, while inverted and right side up. As previously discussed, dolphins are social learners and they exhibit both behavioral and vocal imitation (Herman, 2002, 2012; Reiss & McCowan, 1993; Reiss et al., 1997); therefore, it is possible that Bayley was copying a behavior that she had just seen Foster frequently exhibiting at the mirror. Thus, Bayley’s behavior could be a case of deferred imitation, which has been reported to be a prerequisite for synchronic imitation, pretend play, and MSR in children (Nielsen & Dissanayake, 2004). Although Bayley was not stationed at the mirror every time Foster produced these behaviors, she was in the same pool, which would have given her ample opportunities to observe his behavior. Young dolphins are often responsible for
the appearance and spread of innovative play behaviors in a social group (Kuczaj, 2006; Kuczaj & Eskelinen, 2014b).

Notably, dolphins are not the only species to exhibit social behavior after they are already exhibiting self-directed behavior. Chimpanzees were previously observed exhibiting social displays and presenting sexual postures at the mirror after it was already concluded that the chimpanzees were showing self-recognition (Povinelli, et al., 1993). Povinelli, et al. (1993), argued that it is possible to see a continuation of individual’s behaviors at the mirror that are social in nature “as part of their interest in their physical appearance and overt behavior (p. 369).” Humans of all ages often exhibit social behavior in front of the mirror. For example, prior to going for a recent interview, while standing in front of a mirror, I practiced what I would say when I introduced myself, what I would wear, and even what type of smile I would display.

**Critical issues in MSR**

Comparisons between previous MSR studies conducted with humans and great apes clearly demonstrate several methodological differences (Bard et al., 2006). These differences not only correspond to the actual process of testing and marking individuals, but also in the criteria used to determine when and whether individuals pass the mark test and if they demonstrate the capacity for MSR based on the criteria used. Analyses from previous studies have relied predominantly on the mark test results to determine the capability for MSR in a species and have spent less time discussing the actual behaviors observed, except to categorize them as social or self-directed or mark-directed. Gallup (1970) created the mark test as a more objective measure of MSR; however, he first argued that showing self-directed behavior was sufficient criteria for determining the presence of this ability in a species (Gallup et al. 1995). Yet the specific self-
directed behaviors exhibited at the mirror are often not well documented, considered, or reported. Gallup (1994) even addressed this neglect stating

I have never maintained that the mark test is the sine qua non of self-recognition. Appropriate behavior in response to unobtrusively applied facial marks that can only be seen in a mirror constitutes a means of validating impressions that arise out of seeing animals use mirrors in ways that suggest they realize that their behavior is the source of the behavior depicted in the reflection. In trying to demonstrate self-recognition in other species, some people appear to have lost sight of this and have focused almost exclusively on the mark test (p. 42).

Species shown to demonstrate a capacity for MSR exhibit compelling self-directed behaviors in front of the mirror; therefore, these behaviors should be given more weight when conducting MSR studies. As a result, the current study focused on conducting a detailed event-based analysis of the individual behaviors produced throughout mirror exposure. Looking more closely at the types and numbers of different behaviors produced and when they occur is useful for making developmental comparisons between individuals of the same species or even when making interspecific comparisons.

Previous studies have noted that there are also issues and potential problems with the mark test and inconsistency in results and have questioned its validity as a sole means of assessing MSR. As I previously discussed, MSR studies with chimpanzees (common & pygmy) and humans have reported that individuals do not always pass the mark test even if they are exhibiting compelling self-directed behaviors (Bard et al., 2006; Povinelli et al., 1993; Swartz & Evans, 1991; Walraven, 1995). In a more recent study with Asian elephants, only one of three elephants passed the mark test; however, results demonstrated that all of the elephants tested exhibited self-directed behaviors at the mirror (Plotnik et al., 2006). In a discussion of mark test results in children, Rochat and Zahavi (2011) suggest that findings similar to those described above should be considered false negatives. They also discuss that there may even be false
positives in some children that do pass the mark test. For example, some children are said to pass the test if they see a mark on their mother’s nose and proceed to point to their own nose (Rochat & Zahavi, 2011).

In contrast to the present study and past studies of MSR in dolphins, in a majority of the MSR studies with humans and chimpanzees, individuals are marked only once and multiple subjects are tested. There are a few exceptions in both studies with humans and chimpanzees: Kärtner, Keller, Chaudhary, and Yovsi (2012) conducted weekly mark tests over 6 weeks on children between the ages of 16 to 18 months from various sociocultural contexts, Nielsen & Dissanayake (2004) conducted mark tests with children every three months between the ages of 12 and 24 months, de Veer et al. (2002) conducted mark tests on chimpanzees that had previously been marked 8 years prior in order to determine if mark tests results endure, and Swartz & Evans (1991) conducted multiple mark tests with chimpanzees given varying amounts of mirror exposure. Some of these studies have shown that individuals may initially pass the mark test, but on subsequent mark tests they fail (de Veer et al., 2002; Miles, 1994; Nielsen & Dissanayake, 2004). These inter-individual differences were also seen with the dolphins in the current study. All three of the dolphins were marked multiple times; however, passing one mark test did not predict that they would pass later mark tests even if they were showing compelling self-directed behaviors. It is possible that being marked, although initially interesting, was no longer meaningful to the dolphins because of the lack of consequences associated with being marked or they become habituated to the mark and the marking process. Testing animals while in a social group may also impact mark test results. For example, Nani did not pass her last 2 mark tests because she never stationed at the mirror following being marked. There were extensive social interactions in the pool during this time and it appeared that Nani was more motivated to interact
with her companions than to engage at the mirror. Most MSR studies in humans and primates have been conducted with solitary individuals or children with a parent present. However, the testing of isolated dolphins was not possible especially in the case of young animals. Isolating individual dolphins from their social group is highly stressful for the entire group and is avoided unless necessary for medical emergencies.

The mark test also becomes problematic when testing animals that are not grooming species or animals, like dolphins, that do not have hands to touch the mark. Dolphins often have rake marks and scarring on their bodies, so placing a novel mark on their body may not be salient or meaningful to them or other conspecifics. The same can be said about the salience of the mark for other non-grooming species like elephants. Asian elephants, a species previously shown to demonstrate MSR (Plotnik et al., 2006), engage in dust bathing (throwing dirt and other items on their body) and often have debris on their bodies. Since chimpanzees were the first species tested by Gallup (1970), the mark test was originally developed with primates in mind. Therefore, observing how often individuals touched the mark in front of the mirror was the most objective way to demonstrate MSR in primate species. One recent study argues that because dolphins are not physically able to touch the mark, results of mark tests conducted in the original dolphin MSR study (Reiss & Marino, 2001) are inconclusive and the authors go on to say that “…it would not be surprising if dolphins were capable of visual self-recognition (p. 122)” (Suddendorf & Butler, 2013). If the last part of that statement is true, it seems hard to understand why it would be difficult to accept that dolphins can demonstrate mark-directed behaviors without touching the mark. In this case, the authors make an a priori judgment that only using a method useful for handed species (or species with morphologies such as trunks that can be used to touch a mark) is valid for demonstrating this capability in non-handed species. Again, compelling self-
directed behaviors exhibited by animals in front of the mirror are being ignored.

**Limitations**

In this study, it was often difficult to distinguish when the dolphins were orienting towards marks on the sides of their head. This is an inherent difficulty in conducting mark tests with non-handed species, such as dolphins that cannot touch the mark. Due to the viewing angle of the camera used to record the behavior at the mirror, researcher’s may make incorrect assumptions regarding how the dolphins should orient towards a specific mark based on their limited view. For example, this occurred when coding Foster’s first mark test session, which was initially scored as ambiguous even though his behavior after being marked was strikingly different from his behavior prior to being marked. During this session, after being marked on the left side of his head, Foster stationed at the edge of the mirror head-on with the left half of his body in the frame of the mirror and repeatedly tilted his body and head to the right, which exposed the left side of his head and the mark to more light. Foster’s behavior was different from what was expected. It was expected that he would orient the left side of his head to the mirror and engage in close eye viewing of the left side of the head where the mark was located. However, Foster did not do this but instead exhibited a very different behavior that exposed the marked area to the mirror and he did so repeatedly in several bouts at the mirror in the post-mark condition. It appears that the way Foster oriented his body at the mirror presented the mark in more light and may have made the mark more salient.

As a result, in future studies it may be helpful to simultaneously videotape the mirror sessions from both the dolphin’s point of view and the researcher’s view behind the mirror. This may give researchers a better idea of the visual perspective of the dolphin while investigating the mark at the mirror. In the current study we attempted to determine the dolphins’ field of view
when looking at the mirror by having a diver in the pool videotape his reflection as he approached the mirror; however, this was done only once at the beginning of the study. It would be more useful to be able to compare both perspectives simultaneously for each session.

Another limitation of this study involved a difficulty in controlling the amount of ambient light in both the pool and the pit. The window in the baseline and control sessions had varying degrees of reflectivity depending on the amount of ambient light present. Even though the hatch to the pit door remained open and the shades to the outside of the exhibit were left open to allow in light, there was often too much of a light differential between the pit and the pool in which the dolphins were swimming. As a result, when coding baseline and control sessions there were times when it was dark in the pit and very light in the pool, creating a better reflective surface, so the dolphins would station at the window and engage in what appeared to be self-directed behaviors. However, this did not impact the overall results of this study because the mirror itself was the best reflective surface.

**Future Research**

Similar to the current study, future studies of MSR should conduct a more in depth analysis of the emergence of all mirror-directed behavior throughout all stages, including the types and frequencies of specific behaviors exhibited in front of the mirror and also any relationships that exist between co-occurring behaviors. Dolphins’ behaviors and movements are fluid, often short in duration, and co-occurring, making it difficult to collect durations. However, the amount of time dolphins spend engaging in specific bouts of behavior can be more informative than the number of behaviors produced, especially when trying to determine motivation. When possible, it would also be beneficial to look at the duration of some of the longer bouts of mirror-directed behaviors because spending more time engaging in specific
behaviors at the mirror may suggest increased motivation to use the mirror as a tool for self viewing.

Because the results of the current study demonstrated that dolphins exhibit self-directed behavior at a young age, future developmental MSR studies with dolphins should also look at the emergence of mirror-directed behaviors from birth onward. During this study two of the dolphins in the social group (Maya & Spirit) became pregnant; the original plan was to expose their calves to a mirror within weeks following their birth and then observe their subsequent behavioral responses; however, due to the deaths of both calves during the first postpartum weeks this was not possible. Also, the level of compelling self-directed behavior exhibited at the mirror by both Bayley and Foster suggests that if they could have been marked earlier, they would have most likely shown mark-directed behavior. As a result, future studies should aim to safely mark dolphin calves as soon as self-directed behavior is being exhibited. This procedure may involve conducting specific training sessions early on with both the calf and the mom to allow for marking the calf in the least stressful manner and to determine the best location for the mark. These studies should keep in mind that the best location for the mark may depend on the tolerance of each individual dolphin being marked.

Past and current findings of MSR in dolphins and prolonged self-directed behavior at the mirror prompt the next question: If given choice and control, would dolphins be motivated to request a mirror to view themselves? Future studies should look at the motivational aspects of mirror-use to determine if dolphins and other animals demonstrating the capacity for MSR would be motivated to request a mirror to view themselves and subsequently interact with it. I conducted a pilot study (from 9/17/12 to 11/28/12) with five of the dolphins (Foster, Beau, Bayley, Chesapeake, & Maya) previously exposed to the mirror in the MSR study in an attempt
to assess the dolphins’ motivation to acquire access to a mirror versus preferred objects by giving them choice and control in using an underwater keyboard equipped with 3-dimensional graphic forms that was used in a previous study (Reiss & McCowan, 1993), and modified for this study. Based on previous research (Reiss, 1983; Reiss & McCowan, 1993) I expected that the dolphins in this study would learn associations and correspondences between the graphic forms and objects via a free choice dolphin-driven procedure. Specifically, I predicted that they would use the keyboard to acquire objects and that the dolphins’ choices would match their preferences. The constraint of having only one mirror necessitated that the dolphins come to the understanding that by choosing the toys first, followed by the mirror, they could subsequently take the toys to the mirror and interact with them. Based on previous MSR studies (Marten & Psarakos, 1994; Sarko et al., 2002) I predicted that the dolphins would take requested toys to the mirror and interact with them.

Results demonstrated that offering choice and control to animals that have a history of extensive training was problematic. When confronted with the underwater keyboard, the dolphins in this pilot study often looked to the researchers and trainers for instructions or cues (via hand signals) for how to behave. In fact, one of the young male dolphins (Foster) appeared to exhibit behaviors indicative of frustration during some of the keyboard sessions. The dolphins were curious about the keyboard since it was a novel object in their environment, but even after weeks of exposure and several attempts by the trainers at the aquarium to shape their behavior to touch hand held boards displaying the visual icons or to approach the keyboard, the dolphins were hesitant to touch the keys. Due to constraints of the dolphin exhibit and husbandry concerns the keyboard could not be left in the dolphins’ exhibit pool unattended to allow them to habituate to the apparatus. It is probable that over time, if given continual access to a keyboard that does
not require the presence of a trainer or researcher and if given more opportunities for choice and control, these dolphins would have started to use the keyboard to select objects.

**Significance of the Research**

The results of this research provide the first ontogenetic data on the age of emergence of MSR and the age at which an older dolphin continues to demonstrate an interest in the mirror. This research provides important insights into how highly encephalized species, like humans, apes, and dolphins compare developmentally with regards to the age of emergence and developmental stages of MSR. Results of this study report the first evidence that self-directed behavior is demonstrated in dolphins at a younger age (5 ½ months & 14 ½ months) than has been previously reported for humans and chimpanzees. Documentation of such socio-cognitive development is critical to our understanding of the evolution of intelligence in the animal world. Confirming the ability for MSR with additional dolphins further supports the claim for cognitive convergence between members of Delphinidae, Hominidae, Elephantidae, and Corvidae. Other contributions of this research include: 1) a more in depth analysis of the emergence of mirror-directed behavior and a reevaluation of the categorization of these behaviors, taking into account context and 2) a discussion of the importance of focusing and relying on compelling self-directed behavior exhibited at the mirror as an indicator of MSR and less reliance on only considering positive mark test results as sufficient evidence for this ability.
## Appendix A

### Bottlenose Dolphin Mirror Self-recognition (MSR) Ethogram

<table>
<thead>
<tr>
<th>Code</th>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Arrive</td>
<td>Dolphin approaches and remains at mirror for more than 3 seconds.</td>
</tr>
<tr>
<td>AR</td>
<td>Arch</td>
<td>Flexing body backwards so head and tail position body into a “u” shape.</td>
</tr>
<tr>
<td>AP</td>
<td>Airplane</td>
<td>Pectoral fins positioned perpendicular to body. Head may be stretched up or head-on.</td>
</tr>
<tr>
<td>BK</td>
<td>Blowhole Kiss</td>
<td>While performing a head butt on mirror blowhole makes contact with mirror and is opened and closed producing suction and a “kissing” sound.</td>
</tr>
<tr>
<td>BP</td>
<td>Bubble Production</td>
<td>Any bubbles that are produced from blowhole or mouth.</td>
</tr>
<tr>
<td>BR</td>
<td>Barrel Roll</td>
<td>In horizontal position body is rotated continuously 360 degrees. Can be once or repetitive.</td>
</tr>
<tr>
<td>BSW</td>
<td>Body Splay Window</td>
<td>Swim up to mirror and in one continuous motion slide ventral surface of body across the window with pectoral fins perpendicular to body and neck stretched up. Can be once or repetitive from any direction.</td>
</tr>
<tr>
<td>C</td>
<td>Circling</td>
<td>Swimming by window repeatedly and returning to window frame within 3 seconds.</td>
</tr>
<tr>
<td>CE</td>
<td>Close Eye</td>
<td>One eye (either left or right) is positioned close to the mirror.</td>
</tr>
<tr>
<td>CS</td>
<td>Corkscrew</td>
<td>Barrel roll in the vertical plane. Can be once or repetitive</td>
</tr>
<tr>
<td>E</td>
<td>Echolocate</td>
<td>Producing clicks at the mirror</td>
</tr>
<tr>
<td>EE</td>
<td>Eye Edge</td>
<td>One eye visible at the edge of window, while stationary.</td>
</tr>
<tr>
<td>HB</td>
<td>Head Butt</td>
<td>Head is stretched down and melon and blowhole makes contact with window in a forceful manner. Often hear a “thump” when head makes contact with window. Can be once or repetitive.</td>
</tr>
<tr>
<td>HJ</td>
<td>Head Jerk</td>
<td>Quick jerky movement of head up</td>
</tr>
<tr>
<td>HO</td>
<td>Head On</td>
<td>Body oriented perpendicular to mirror with head facing mirror and stationary.</td>
</tr>
<tr>
<td>HR</td>
<td>Head Rotation</td>
<td>Circular movement of only head, clockwise or counterclockwise. Can be once or repetitive.</td>
</tr>
<tr>
<td>HS</td>
<td>Head Stand</td>
<td>Dorsal side of body facing mirror, positioned vertically with head oriented at the bottom of the mirror.</td>
</tr>
<tr>
<td>HT</td>
<td>Head Tilt</td>
<td>Body vertical with small movement of head to left or right. Can be once or repetitive.</td>
</tr>
<tr>
<td>HBT</td>
<td>Horizontal Body Tilt</td>
<td>In horizontal position body is rotated 90 to 180 degrees.</td>
</tr>
<tr>
<td>Code</td>
<td>Description</td>
<td>Definition</td>
</tr>
<tr>
<td>------</td>
<td>------------------------------</td>
<td>---------------------------------------------------------------------------</td>
</tr>
<tr>
<td>HHM</td>
<td>Horizontal Head Movement</td>
<td>Head moved in horizontal plane from left to right. Can be once or repetitive.</td>
</tr>
<tr>
<td>JC</td>
<td>Jaw Clap</td>
<td>Quick forceful closing of lower and upper jaw creating a loud popping sound</td>
</tr>
<tr>
<td>LBR</td>
<td>Lateral Body Rub</td>
<td>Dolphin rubs left or right side of head and body against window, often accompanied by rostrum contact and often when vertical.</td>
</tr>
<tr>
<td>L</td>
<td>Leave</td>
<td>Dolphin leaves mirror and does not return within 3 seconds.</td>
</tr>
<tr>
<td>NF</td>
<td>Near and Far</td>
<td>Swim up to mirror and then away from mirror in same plane. Also used when dolphin pushes off the mirror with head and then floats away.</td>
</tr>
<tr>
<td>NS</td>
<td>Neck Stretch</td>
<td>Extension of neck to move head up or down. Can be once or repetitive.</td>
</tr>
<tr>
<td>OM</td>
<td>Open Mouth</td>
<td>Mouth open can be a small amount or a large amount (wide).</td>
</tr>
<tr>
<td>O</td>
<td>Orient</td>
<td>Dolphin is stationary and the head is positioned either to the left (L) or right (R). Dolphins’ body can be vertical or head-on</td>
</tr>
<tr>
<td>PB</td>
<td>Peek-a-boo</td>
<td>Moving head/eye in and out of mirror frame. Can be once or repetitive.</td>
</tr>
<tr>
<td>PD</td>
<td>Penis Display</td>
<td>Protrusion/protration of penis while at the mirror.</td>
</tr>
<tr>
<td>PS</td>
<td>Pec Shimmy</td>
<td>Repeated movement of one or both pectoral fins. Body may be positioned in either vertical or horizontal plane.</td>
</tr>
<tr>
<td>QJ</td>
<td>Quiver Jerk</td>
<td>Sudden jerky movement of entire body.</td>
</tr>
<tr>
<td>RC</td>
<td>Rostrum Contact</td>
<td>End of rostrum touches window, often causing a “squeak” sound like a squeegee rubbing the glass.</td>
</tr>
<tr>
<td>RH</td>
<td>Rocking Horse</td>
<td>In vertical position, beginning with head, body is rocked forward 90 degrees and then backward to starting position. Can be once or repetitive.</td>
</tr>
<tr>
<td>SH</td>
<td>Spy Hopping</td>
<td>Dolphin’s body is vertical as they move up to surface and back down. Head goes past surface of water.</td>
</tr>
<tr>
<td>SB</td>
<td>Swim By</td>
<td>Swim by window slowly (at least 3 seconds or more) often accompanied by dolphin looking into mirror.</td>
</tr>
<tr>
<td>SS</td>
<td>Somersault</td>
<td>In vertical or horizontal plane, beginning with head, body is rocked forward and continues 360 degrees.</td>
</tr>
<tr>
<td>ST</td>
<td>Station</td>
<td>Body is positioned at mirror and not moving. Body can be vertical (dorsal or ventral facing mirror) or parallel (only one side of body facing mirror).</td>
</tr>
<tr>
<td>SST</td>
<td>Short Station</td>
<td>Brief (&lt;4 sec) stationing at mirror</td>
</tr>
<tr>
<td>SW</td>
<td>Stevie Wonder</td>
<td>Body vertical with neck stretched up and moving head from side to side in a swaying motion.</td>
</tr>
<tr>
<td>VBT</td>
<td>Vertical Body Tilt</td>
<td>Body oriented vertically and is moved side to side in a pendulum manner.</td>
</tr>
<tr>
<td>VHM</td>
<td>Vertical Head Movement</td>
<td>Head moved in vertical plane up and down. Can be once or repetitive.</td>
</tr>
<tr>
<td>WBS</td>
<td>Whistle Bubble Stream</td>
<td>Auditory sound produced by blowhole with visible stream of bubbles.</td>
</tr>
<tr>
<td>-----</td>
<td>-----------------------</td>
<td>--------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>YW</td>
<td>Yaw</td>
<td>Producing a squawky vocal, mouth can be open or closed.</td>
</tr>
</tbody>
</table>

**Modifiers (Put before or after behavior codes)**

<table>
<thead>
<tr>
<th>Modifier</th>
<th>Description</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>Distant</td>
<td>Dolphin is oriented towards mirror approximately 5 feet away.</td>
</tr>
<tr>
<td>Dr</td>
<td>Dorsal</td>
<td>Modifier put after behavior code.</td>
</tr>
<tr>
<td>I</td>
<td>Inverted</td>
<td>Modifier put before behavior code.</td>
</tr>
<tr>
<td>L</td>
<td>Left</td>
<td>Modifier put before behavior code.</td>
</tr>
<tr>
<td>PI</td>
<td>Partial Inverted</td>
<td>Modifier put before behavior code</td>
</tr>
<tr>
<td>R</td>
<td>Repetitive</td>
<td>Repeating a single behavior at least twice. Modifier put before behavior code</td>
</tr>
<tr>
<td>R</td>
<td>Right</td>
<td>Modifier put before behavior code.</td>
</tr>
<tr>
<td>S</td>
<td>Small</td>
<td>Modifier put after open mouth (OMS).</td>
</tr>
<tr>
<td>V</td>
<td>Ventral</td>
<td>Modifier put after behavior code.</td>
</tr>
<tr>
<td>W</td>
<td>Wide</td>
<td>Modifier put after open mouth (OMW).</td>
</tr>
</tbody>
</table>
Bottlenose Dolphin Bubble Behavior at Mirror Ethogram

<table>
<thead>
<tr>
<th>Code</th>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Ambiguous</td>
<td>Bubble formation unclear due to visibility</td>
</tr>
<tr>
<td>BB</td>
<td>Bubble Burst</td>
<td>Large number of bubbles released simultaneously, typically in a shape similar to a mushroom cloud.</td>
</tr>
<tr>
<td>hbBB</td>
<td>Head Butt and Bubble Burst</td>
<td>Dolphin’s melon makes contact with window while simultaneously releasing bubble burst.</td>
</tr>
<tr>
<td>iBB</td>
<td>Inverted Bubble Burst</td>
<td>Large number of bubbles released simultaneously, typically in a shape similar to a mushroom cloud, while body is in an inverted position.</td>
</tr>
<tr>
<td>BS</td>
<td>Bubble Stream</td>
<td>Line of single bubbles released continuously.</td>
</tr>
<tr>
<td>hbBS</td>
<td>Head Butt and Bubble Stream</td>
<td>Dolphin’s melon makes contact with window, while simultaneously releasing line of single bubbles released continuously.</td>
</tr>
<tr>
<td>iBS</td>
<td>Inverted Bubble Stream</td>
<td>Line of single bubbles released continuously, while body is in an inverted position.</td>
</tr>
<tr>
<td>OB</td>
<td>One Bubble</td>
<td>Single bubble produced.</td>
</tr>
<tr>
<td>HBO</td>
<td>Head Butt and One Bubble</td>
<td>Dolphin’s melon makes contact with window while simultaneously releasing one bubble.</td>
</tr>
<tr>
<td>iOB</td>
<td>Inverted One Bubble</td>
<td>Single bubble produced, while body is in an inverted position.</td>
</tr>
<tr>
<td>BM</td>
<td>Bubble Multiple</td>
<td>Multiple bubbles produced.</td>
</tr>
<tr>
<td>HBM</td>
<td>Head Butt and Bubble Multiple</td>
<td>Dolphin’s melon makes contact with window while simultaneously releasing several bubbles.</td>
</tr>
<tr>
<td>iBM</td>
<td>Inverted Bubble Multiple</td>
<td>Multiple bubbles produced, while body is in an inverted position.</td>
</tr>
<tr>
<td>SB</td>
<td>Smash Bubble</td>
<td>Dolphin produces a bubble burst or multiple bubbles, and then rapidly smashes head/rostrum (sometimes biting) into the bubbles bursting it/creating cloud of bubbles.</td>
</tr>
<tr>
<td>iSB</td>
<td>Inverted Smash Bubble</td>
<td>Dolphin produces a bubble burst or multiple bubbles, and then rapidly smashes head/rostrum (sometimes biting) into the bubbles bursting it/creating cloud of bubbles, while body is in an inverted position.</td>
</tr>
<tr>
<td>BR</td>
<td>Bubble Ring</td>
<td>Air bubble with ring formation (McCowan, Marino, Vance, Walke &amp; Reiss, 2000).</td>
</tr>
<tr>
<td>pBR</td>
<td>Partial Bubble Ring</td>
<td>Air bubble with imperfect ring formation.</td>
</tr>
<tr>
<td>MB</td>
<td>Mouth Bubble</td>
<td>Bubble(s) released not from the blowhole, but from the mouth.</td>
</tr>
<tr>
<td>BC</td>
<td>Bubble Cord</td>
<td>Long thin bubble often trailing behind a bubble burst.</td>
</tr>
</tbody>
</table>
References


Pace, D. S. (2000). Fluke-made bubble rings as toys in bottlenose dolphin calves (*Tursiops truncates*). *Aquatic Mammals, 26*(1), 57-64.


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*PNAS, 103*(45), 17053-17057.


*Journal of Comparative Psychology, 107*, 347-372.


