*International Journal of Comparative Psychology*, 2010, 23, 701-722.


# Play in Wild and Captive Cetaceans

**Robin D. Paulos, Marie Trone, and Stan A. Kuczaj II**
***University of Southern Mississippi, U.S.A.***

Although play behavior is difficult to define, it has been abundantly documented in the cetacean literature. Play behavior is prevalent among the various taxa and is exhibited by individuals of all age classes. However, it is often difficult to follow individuals, observe underwater behavior, and obtain multiple sightings of individuals when investigating free-ranging populations. Captive studies allow for the systematic manipulation of variables and the collection of detailed data with regard to individuals, age, and gender by being able to observe behavior both at the surface and underwater. Pooling information from both wild and captive studies of play allows for more robust theories, conclusions and understanding. In this paper, we provide a review of play behavior in both wild and captive cetacean populations as a first step toward a more complete understanding of the significance of cetacean play.

The ability to study a particular phenomenon in both wild and captive populations of animals provides a greater depth of knowledge than would be possible with data gleaned from only one population type. The study of wild animals is typically based on naturalistic observation and although these types of studies provide a magnificent window into the lives of free-ranging animals and are a crucial component in the study of behavior, they often do not allow for true experimental design with the ability to manipulate variables. The study of captive animals provides this valuable scientific component. Therefore, combining studies of wild animals with those of captive individuals results in a more comprehensive understanding of the behaviors in question. Indeed, studies from wild and captive populations have provided insight into the lives of numerous species of animals (e.g., Brown & Norris, 1956; Saayman, Tayler, & Bower, 1973; Veasey, Waran, & Young, 1996). To illustrate the value of this approach for the study of cetacean behavior, we explore the contributions of studies of play in both wild and captive cetaceans.

The study of play in animals has been a subject of interest to scholars for many years (Bekoff & Allen, 1998; Bekoff & Byers, 1981; Bel'kovich, Ivanova, Kozarovitsky, Novikova, & Kharitonov, 1991; Burghardt, 2005; Caro, 1995; Coelho & Bramblett, 1982; Delfour & Aulagnier, 1997; Fagen, 1993; Ficken, 1977; Gewalt, 1989; Groos, 1898; Guinet, 1991; Harcourt, 1991; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Kuczaj & Trone, 2001; Kuyk, Dazey, & Erwin, 1976; Markus & Croft, 1995; McCowan, Marino, Vance, Walke, & Reiss, 2000; Muller-Schwarze, Stagge, & Muller-Schwarze, 1982; Ortega & Beckoff, 1987; Power, 2000; Spinka, Newberry, & Bekoff, 2001; Thompson, 1996; West, 1974; Würsig, Dorsey, Richardson, & Wells, 1989). Although it seems we are adept at recognizing play when we see it, we are exceptionally inexpert at defining the term. Despite this definitional deficiency, behaviors that have been

Correspondence concerning this article should be addressed to Robin Paulos, University of Southern Mississippi, Department of Psychology, 118 College Drive, 5025, Hattiesburg, MS 39406, U.S.A. (robin.paulos@gmail.com).

characterized as play have been observed in a diverse group of animals including reptiles, birds, and invertebrates as well as mammals. While many species exhibit play behaviors, a survey of these animals and the resulting phylogenetic trees indicates that play is a diverse phenomenon that appears to have evolved independently in a variety of species (Burghardt, 2005), suggesting that play is an important aspect of behavioral ontogeny for many species. If so, play may facilitate an individual's ability to adapt to changing environments and so contribute to the continued survival of species (Kuczaj & Makecha, 2008).

Explanations of why animals play abound in the literature (for an overview see Beckoff & Allen, 1998; Burghardt, 2005; Bornstein & O'Reilly, 1993; Bruner, 1972, 1973; Fagan, 1981; Garvey, 1974; Groos, 1898; Kuczaj et al., 2006; Piaget, 1951, 1952; Spinka et al., 2001; Vanderberg, 1978). Play may help animals acquire knowledge of objects or other aspects of their environment. It may also provide a mechanism by which young animals perfect motor skills through the use of practice. Play can facilitate the development of flexible problem solving skills by providing a non-threatening context in which animals can explore the consequences of new behaviors (Kuczaj et al., 2006; Kuczaj & Makecha, 2008; Kuczaj & Trone, 2001; Rose, 1992; West, 1974). Play can also provide young animals a venue in which they cultivate important social relationships (Bekoff & Byers, 1981; Coelho & Bramblett, 1982; Colvin & Tissler, 1985; Connor, Wells, Mann, & Read, 2000; Miller & Nadler, 1982; Thompson, 1996; Walters, 1987).

Play behavior is prevalent among the various cetacean taxa and is common among young animals, as well as in mature individuals. Play can be solitary and involve only the playing animal. Play can also be social when two or more animals are playing together. But as Parten (1932) noted, it is important to distinguish social play from parallel play. Social play involves some form of cooperation among the play partners, whereas parallel play occurs when individuals are playing in the same vicinity but are not really playing together. Parallel play, then, is a form of solitary play even though it occurs in a social context. Play can be self-directed (such as locomotor play in which movement of the individual is the focus) or directed at an object or another animal (Bel'kovich et al., 1991). Published accounts of play behavior in cetaceans range from anecdotal reports to detailed studies that suggest capacities such as self-monitoring, planning, innovation, imitation and cultural transmission.

## Locomotor Play

Cetaceans engage in a variety of locomotor play, including aerial behaviors, erratic swimming, stranding, and surfing. Aerial behaviors consist of leaps, breaches, flips, pinwheels, and slapping the surface of the water with various body parts such as the chin, pectoral fin, or tail flukes. Erratic swimming is characterized by sudden changes in direction, spiraling during forward movement, swimming upside-down or on one's side. Stranding occurs when a cetacean purposefully propels its body out of the water onto a sloping beach. Surfing transpires when a dolphin rides the pressure wave produced by a boat, ship, or a

baleen whale. While in some situations these behaviors may have utilitarian purposes, in other circumstances they seem playful.

***Aerial behavior play***

Dusky dolphins (*Lagenorhynchus obscurus*) typically engage in vigorous aerial behaviors during feeding and post-feeding activities. Given that the water is relatively shallow, averaging a depth of 40 m in foraging areas, Würsig and Würsig (1980) suggested that the aerial activity of the dusky dolphins keeps their prey near the surface of the water. Alternatively, Würsig and Würsig (1980) also proposed that this aerial behavior may serve to attract conspecifics to the feeding site to assist in cooperative feeding.

Given that bottlenose dolphins (*Tursiops truncatus*) hunting in Doubtful Sound, New Zealand display similar aerial behaviors during feeding in waters with an average depth of 200 m, these behaviors probably do not function in herding fish (Lusseau, 2006). Furthermore, changes in bottlenose dolphin group activities (i.e., traveling, resting, milling, diving and socializing) have been associated with increased aerial behaviors displayed primarily by a few individuals (Lusseau, 2006). The percussive sounds that result from aerial behaviors do not propagate underwater nearly as far as whale and dolphin vocalizations (Finneran et al., 2000). These aerial behaviors may function to signal other pod members without alerting competing conspecifics, prey or predators (Lusseau, 2006).

In addition to having a foraging or communicative function, aerial behavior may also be an aspect of locomotor play displayed by both mysticetes and odontocetes. For example, in one study of the behavioral development of southern right whales (*Eubalaena australis*), calves began executing behaviors such as breaches, erratic swimming, pectoral fin and tail slapping within 30 to 63 days of life (Thomas & Taber, 1984). These activities were categorized as play and were the second most common behavior observed, following traveling. Mothers discouraged their calves from engaging in these play activities by pinning the calves to the bottom or rolling upside down and carrying the calves on their chests. The mothers may have curtailed these play behaviors because they did not fulfill an immediate need for the calves yet resulted in the reduction of energy reserves of the fasting mother.

Another potential play behavior exhibited by southern right whales and bowhead whales (*Balaena mysticetus*) involves suspending the tail flukes above the surface of the water for extended periods of time (Payne, 1995; Würsig, 2002). This behavior could function in cooling the whales (Payne, 1995; Würsig, 2002). However, Payne (1995) also hypothesized that these whales may be engaging in a form of play, utilizing their tails for sailing purposes.

High-energy surface behaviors displayed by various odontocete species have also been described anecdotally as play. For example, airborne activities exhibited by bottlenose dolphins in the Black Sea have been categorized as play, as they rarely occurred during migration or hunting (Bel'kovich et al., 1991). Würsig and Würsig (1979) reported that juvenile bottlenose dolphins and calves in

Argentina engaged in leaps that resulted in considerable splashing and sound production three times as often as adults, and suggested these behaviors were play.

Fagen (1981) reported that younger animals tend to play more than adults. Furthermore, it has been demonstrated that play behaviors are more prevalent once dietary needs have been fulfilled (Muller-Schwarze et al., 1982; Sommer & Mendoza-Granados, 1995). Würsig and Würsig (1980) suggested that dusky dolphin aerial behavior might be classified as play because it is observed during hunting but continues for some time following feeding bouts. Additional evidence for this hypothesis is suggested by the increased frequencies of aerial behavior exhibited by both free-ranging and captive bottlenose dolphins (Bel'kovich et al., 1991; Trone, Kuczaj, & Solangi, 2005), as well as captive common dolphins (*Delphinus delphis*) (Kyngdon, Minot, & Stafford, 2003) following feeds.

***Intentional stranding play***

Intentional stranding is another form of locomotor cetacean play behavior that has been studied in the wild. At Possession Island in the Crozet Archipelago, five adult female killer whales (*Orcinus orca*) were observed to intentionally beach themselves. Even though these females occasionally captured elephant seal (*Mirounga leonia*) pups, the author classified this behavior as social beaching play when executed in tandem with other whales (Guinet, 1991). Two calves were observed with these five females. One calf was three years old and the other was four years old the first time they were seen to accompany adults in social beaching play. Both calves were five years old the first time they stranded themselves alone. This behavior was considered play since the calves beached themselves 81 times in the absence of potential prey, and only seven times when seals were present. Moreover, one of the whales was six years old before it actually captured its first seal (Guinet & Bouvier, 1995).

Similarly, captive bottlenose dolphins have been reported to engage in voluntary beaching play (DeLong, 1999; Kuczaj et al., 2006). Members of the Marine Mammal Behavior and Cognition Laboratory at the University of Southern Mississippi have observed intentional beaching in the course of studying the development of dolphin play behavior. One of the calves that this group observed was 2 years 3 months old the first time he was observed to beach himself on a dock. This event occurred two and a half months after he observed his mother beach herself. Three other calves were also present in the pool during this time. These three calves (aged 2 years 7 months to 3 years 1 month) all beached themselves for the first time within a two week period. Thus, both captive and wild cetaceans have been documented to begin intentional stranding between two and four years of age, typically after they have observed another animal engaging in such behavior.

### *Surfing play*

Wild bottlenose dolphins seem to surf as play, repeatedly riding waves into shore. Surfing incidents have been reported world-wide, including Florida (Caldwell & Fields, 1959), Plettenberg Bay, Africa (Saayman et al., 1973), Golfo San Jose, Argentina (Würsig & Würsig, 1979), Puerto Peñasco, Baja California (Norris & Dohl, 1980), the Black Sea (Bel'kovich et al., 1991), and San Diego, California (Hanson & Defran, 1993). Feeding was only implicated in the San Diego incident. At this location where various prey species inhabit the surf zone, the dolphins were seen to submerge near the shoreline, and pelicans (*Pelecanus occidentalis*) were observed to dive in close proximity to the dolphins (Hanson & Defran, 1993). The diving pelicans were taken to be an indication that fish were present.

Surfing behavior of the tucuxi (*Sotalia fluviatilis*) has been documented as play in Brazil. Spinelli, Nascimento, and Yamamoto (2002) reported that these animals also executed a variety of aerial behaviors while surfing. As there were no evident utilitarian goals associated with these behavioral episodes, the authors concluded that this surfing was play.

Some odontocete species are notorious for surfing the pressure wave produced by boats. Play has been implied in these cases since feeding is not observed and often the animals change their course of travel to intercept passing watercraft. Bel'kovich et al. (1991) documented this behavior for bottlenose dolphins in the Black Sea. Würsig and Würsig (1979) further reported that bottlenose dolphins interacted with the pressure wave 9.5% of the times that the dolphins approached the researcher's boat. Dusky dolphins have been documented to travel as far as 2 to 3 km in order to intercept vessels and surf the resultant pressure waves (Würsig, 2002; Würsig & Würsig, 1980). However, dusky dolphins only engaged in this behavior following feeding bouts (Würsig & Würsig, 1980). Finally, rough-toothed dolphins (*Steno bredanensis*) were reported to spend 17.5 % of the time that they were observed to be either riding the bow or wake wave produced by the research boat (Kuczaj & Yeater, 2007).

Bottlenose dolphins ride the pressure waves produced by other species of cetacean as well as those produced by boats. Dolphins have been observed surfing the resultant pressure waves of swimming southern right whales and sperm whales (*Physeter macrocephalus*) (Würsig, 2002; Würsig & Würsig, 1979). As is often the case with boats, dolphins have been observed to change their direction of travel by up to 300 m to intercept a passing whale. When the whales were swimming too slowly to produce a strong pressure wave, the dolphins swam perpendicularly towards the heads of the whales in 24 of the 26 incidents. These actions appeared to annoy the whales, as the whales chuffed and lunged forward. The dolphins then continued their surfing activity in the renewed pressure waves. This intriguing observation demonstrates that dolphins do more than take advantage of existing waves to surf. They sometimes take actions to produce the waves they need to play. Of course, it is difficult to determine if the dolphins are intentionally planning their behavior in this context (see Kuczaj, Xitco, & Gory this issue, for a

consideration of dolphin planning), but the dolphins' behavior is certainly reminiscent of planning behavior.

It is not possible for captive dolphins to surf or ride the pressure waves produced by boats or baleen whales. However, one of the authors (MT) has observed captive bottlenose dolphins surfing waves produced by hurricane-force winds when residing in open-ocean lagoons. This author has also witnessed dolphins quickly towing inflatable pool toys, releasing the toy, and then riding the subsequent pressure waves. Surfing appears to be a ubiquitous play behavior of dolphins, regardless of whether they reside in the open ocean or a captive environment.

## Social Play

Solitary cetaceans exhibit locomotor play behaviors, but two or more individuals may engage in these play behaviors simultaneously. These animals may be acting in parallel, as is the case of free-ranging killer whales intentionally stranding in groups (Guinet, 1991; Parten, 1932). However, these cetaceans may be engaged in social play, cooperating while playing with airborne antics, erratic swimming, chasing, and tactile interactions. For example, the Marine Mammal Behavior and Cognition Laboratory at the University of Southern Mississippi has documented social play when bottlenose dolphin calves intentionally beach themselves on docks. Specifically, after one dolphin propels itself out of the water and onto a dock, other calves push and nudge the beached dolphin back into the water. In the wild, species that have been reported to participate in social play include the bottlenose dolphin (Bel'kovich et al., 1991; Connor et al., 2000; Mann & Smuts, 1999), dusky dolphin (Würsig, 2002; Würsig, & Würsig, 1980), Hector's dolphin (*Cephalorhynchus hectori*) (Slooten, 1994), humpback dolphin (*Sousa* sp.) (Saayman & Tayler, 1973), and the tucuxi (Spinelli et al., 2002). Species that have been reported to engage in social play in captivity include the bottlenose dolphin (Bel'kovich, Krushinskaya, & Gurevich, 1970; Tizzi, Castellano, & Pace, 2001), Pacific bottlenose dolphin (*Tursiops gilli*) (Defran & Pryor, 1980), common dolphin (Defran & Pryor, 1980), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) (Defran & Pryor, 1980), killer whale (Defran & Pryor, 1980), spinner dolphin (*Stenella longirostris*) (Defran & Pryor, 1980), and the Amazon River dolphin (*Inia geoffrensis*) (Sylvestre, 1985).

Subadult and juvenile male northern resident killer whales have been documented partaking in social play. These males engaged in frequent body contact and sexually oriented behaviors within small groups (Rose, 1992). Furthermore, adolescents participated in such interactions four times as often as adults. Rose suggested that these associations may help adolescents gain skill in courtship activities.

Similar social play behavior has been observed among a group of juvenile bottlenose dolphins in Shark Bay, Australia. In this population of dolphins, adult males regularly form alliances and herd females for breeding purposes, (Connor et al., 2000). However, during a documented episode of play herding, one juvenile of

unknown sex was seen to switch roles and participate as the herded dolphin as well as the pursuing dolphin. The group dispersed following the play episode, whereas in true adult herding, the herding occurs in conjunction with other activities such as foraging, traveling and resting (Connor et al., 2000). In this situation, the play activities may assist to foster the cultivation of important social relationships as well as provide practice in the different roles.

A sub-population of the Shark Bay dolphins has been studied at Monkey Mia, where the dolphins frequent the beach and receive dead fish provisioned by humans. This unique situation has permitted researchers to document the ontogeny of calf play behavior (Mann & Smuts, 1999). At Monkey Mia, social play has been observed occasionally within the first week of life, but occurs more frequently after four weeks. The social play observed has included calves engaging in reciprocal chasing with other calves as well as with their own mothers.

Similar results have been obtained from investigations of captive bottlenose dolphins. For example, reciprocal pushing behavior between young animals has been documented (Bel'kovich et al., 1970; Kuczaj & Makecha, 2008). Moreover, dolphin calves engage in more social play with other calves than they do with adults (DeLong, 1999; Tizzi et al., 2001). Finally, chasing was the predominant form of social play observed by Tizzi et al. (2001), constituting approximately 68% of the social play behaviors that were observed.

The above studies show parallels between the locomotor and social play of both wild and captive cetaceans. Characteristics of play are shared among species as diverse as bowhead whales, bottlenose dolphins and river dolphins. Interestingly, isolated populations devise similar games, some of which seem to involve cooperation and planning. These properties also extend to play with objects as described below.

## Object Play

Wild and captive cetaceans show a natural inclination to manipulate objects encountered in their environment. Organic items such as large logs, kelp, feathers and even other animal species may be the focus of this play behavior. Man-made items such as plastic bags, coins, cleaning equipment, broken tiles, balls, hoops, and rings also catch the attention of cetaceans. Furthermore, they create their own toys. For example, dolphins manufacture and modify bubbles and bubble rings during play. Odontocetes also have been observed harassing various species of other cetaceans, pinnipeds, birds, sea turtles, and live fish, as well as dead fish provided to them by humans as food. Examples of these four categories of object play (natural objects, man-made objects, bubbles, and other species) will be explored in the following sections.

### *Natural object play*

Bowhead whales have been reported to interact with logs measuring up to 10 m in length on the summer-fall feeding grounds in the Beaufort Sea (Würsig et

al., 1989). These whales balance the logs on their backs and bellies, lift the logs as high as 3-5 m out of the water, push the logs with their heads and bodies, and force the logs underwater. These bouts of activity last anywhere from 5 seconds to 1.5 hours and have been categorized as play. The manner in which the whales interact with the logs is similar to that seen in bouts of sexual behavior (Würsig, 2002; Würsig et al., 1989), as well as maternal discipline (Payne, 1995).

Seaweed is often manipulated by wild cetaceans. Bottlenose dolphins in England (Bloom, 1991) and in Argentina (Würsig & Würsig, 1979) carry kelp on the melon, pectoral flipper or tail flukes with the kelp often passed between body parts. Dusky dolphins (Würsig, 2002; Würsig & Würsig, 1980) and rough-toothed dolphins (Kuczaj & Yeater, 2007) also engage in this activity, sometimes carrying and passing seaweed between individuals. Hector's dolphins (Slooten & Dawson, 1994), Atlantic spotted dolphins (*Stenella frontalis*) (Miles & Herzing, 2003), and rough-toothed dolphins (Kuczaj & Yeater, 2007) also have been documented to carry seagrass using various body parts.

Similarly, the wild tucuxi also playfully interact with algae and sticks (Spinelli et al., 2002). Although the Amazon River dolphin shares the same habitat as the tucuxi, only adult males interact with objects such as aquatic plants and balls of clay. Furthermore, they are more likely to do so in the presence of females and are 40 times more likely to aggressively interact with other males that possess such objects. However, object manipulation in this case may be a form of male display and not related to play behavior (Martin, da Silva, & Rothery, 2008).

Although the above accounts of interactions with biological objects appear to be play, interactions with naturally occurring objects cannot always be classified as such. Manipulation of sea sponges appears to be a form of tool use demonstrated by two species of free-ranging dolphins. In Shark Bay, Australia, five female bottlenose dolphins were regularly observed carrying sponges on their rostra (Smolker, Richards, Conner, Mann, & Berggren, 1997). Similarly, in Hinchinbrook Channel, Australia, an Indo-Pacific humpback dolphin (*Sousa chinensis*) was also observed carrying a sponge (Parra, 2007). The nature of the sponge-carrying dolphins was stereotypical and lacked the aerial behavior often associated with play bouts. Therefore, both reports propose that the sponges were used for protection of the rostrum from abrasive materials on the sea floor while foraging for benthic prey and were not objects of play (Parra, 2007; Smolker et al., 1997).

Like their wild counterparts, captive cetaceans creatively interact with natural objects that they encounter in their environment. Solitary dolphins spontaneously release feathers into water jets that resulted in the feathers being quickly returned to the waiting dolphins (Brown & Norris, 1956; Kuczaj et al., 2006; Tavolga, 1966). Indeed, in one case the dolphins actively plucked the feathers from pelicans floating on the surface of the water (Brown & Norris, 1956). Tavolga (1966) reported that dolphins cooperatively participated in this game. One dolphin was stationed close to the water jet and released the feather while a second dolphin positioned itself further away to intercept the fast-moving feather. Once caught, the intercepting dolphin changed places and roles with the original feather-

releasing dolphin. Although mothers partook in this game with their calves, generally two juveniles were the participants (Tavolga, 1966).

***Man-made object play***

Wild cetaceans engage in cooperative play using not only the organic objects just discussed, but man-made objects encountered in their environment as well. One report described an incident that involved a juvenile and two adult rough-toothed dolphins (Kuczaj & Highfill, 2005; Kuczaj & Yeater, 2007). These animals were manipulating a piece of plastic similar to the way they might interact with a piece of seaweed or seagrass, carrying it with their mouths, pectoral fins and tail flukes. The dolphins took turns passing the plastic from one to the other while swimming in a group. The adults released the plastic close to the juvenile's mouth several times, thus facilitating the juvenile's acquisition of the object.

Captive dolphins also manipulate flaccid, man-made objects as if they were seaweed or seagrass. Some of these objects may be intentionally given to the animals as toys. For example, Prescott (1968) in a personal communication to the Caldwells, reported that he had given small towels to a Hawaiian spinner dolphin (*Stenella* sp.) while she was housed in a pool alone (Caldwell & Caldwell, 1972). However, most often these items accidentally fall into the dolphins' pools. Some examples of such objects include tape, bandages, gauze, rope, plastic foam, and scarves (Bel'kovich et al., 1970; Kuczaj et al., 2006; Tavolga, 1966). Indeed, almost any object encountered in a cetacean pool becomes a toy. Other objects that have accidentally become the focus of dolphin play activities include wallets, hats (Tavolga, 1966), pieces of wood (Bel'kovich et al., 1970), coins (Caldwell & Caldwell, 1972), pool cleaning equipment (Gewalt, 1989; Tayler & Saayman, 1973), and sunglasses (Kuczaj et al., 2006).

Manmade objects are often presented to captive cetaceans as toys for environmental enrichment purposes. When available, balls seem to be a popular choice as play objects (Bel'kovich et al., 1970; Brown & Norris, 1956; Norris & Dohl, 1980). However, cetaceans also play with plastic bats, knotted ropes, buoys, buckets, basketballs, and water-filled balls of various types (Kuczaj et al., 2002, 2006).

In a longitudinal study conducted over a five-year period of the development of captive bottlenose dolphin play behavior, Kuczaj and colleagues (2006) categorized play behaviors as follows: motor play, bubble play, human play, ball play, and object play (with objects other than balls). Thus, objects that inadvertently fell into the pool as well as those that were purposely given to the dolphins were considered in the analyses. During the course of this study 270 novel play behaviors were documented. Calves were responsible for 220 of these novel behaviors, and 163 of these calf-initiated novel behaviors were subsequently reproduced by other dolphins. Calves were significantly more likely to mimic these novel play behaviors than were the adults residing in the same pool. Moreover, both calves and adults were more likely to mimic a novel play behavior produced by a calf rather than one generated by another adult. The calves in this study

favored mimicking novel play behaviors originated by other adults over those initiated by their own mothers. Based on these data, the authors proposed that calves were the primary source of cultural innovation and cultural transmission of play behaviors in this captive population (Kuczaj et al., 2006; Kuczaj & Walker, 2006).

***Bubble play***

Bubble play is relatively infrequent compared to other forms of play and is most often reported in studies of captive animals (Delfour & Aulagnier, 1997: Kuczaj et al., 2006). Wild belugas (*Delphinapterus leucas*) and Atlantic and Pacific spotted dolphins (*Stenella attenuata*) have been reported to produce bubble rings, but there is no evidence that this is done for recreational purposes (Marten, Shariff, Psarakos, & White, 1996). However, captive Amazon River dolphins, beluga whales, and bottlenose dolphins play with self-produced bubbles (Delfour & Aulagnier, 1997; Gewalt, 1989; Kuczaj et al., 2006; Kuczaj & Walker, 2006; McCowan et al., 2000; Pace, 2000; Tizzi et al., 2001). Bubble play does not appear to be limited by age or sex, as the youngest cetacean documented to engage in this behavior is a 1-month-old bottlenose dolphin calf (Tizzi et al., 2001), and the oldest is a 37-year-old beluga whale (Delfour & Aulagnier, 1997). Bubble play appears to occur with similar frequency in both sexes. Although bubble play is not the most commonly observed play behavior, cetaceans creatively interact with their bubble fabrications (Kuczaj & Walker, 2006).

Cetaceans in captivity demonstrate ingenuity in the variety of ways they create different bubble toys. Amazon River dolphins produced bubble curtains by smacking the surface of the water with an elongated stick held in the dolphin's mouth then proceeded to swim through their creation (Gewalt, 1989). Impressively, two Amazon River dolphins have been observed cooperatively engaging in this behavior, with one producing the bubble curtain and the other swimming through the rising bubbles (Gewalt, 1989). Although it is not clear why the dolphins engage in this behavior, it is possible that swimming through the rising bubbles provides a unique form of tactile stimulation.

Bubble rings are another type of bubble toy and are produced in a variety of ways. Some bottlenose dolphins and Amazon River dolphins create bubble rings by simply releasing air from the blowhole (Gewalt, 1989; Marten et al., 1996), while some belugas and Amazon River dolphins create bubble rings by releasing air that is trapped within their mouths (Delfour & Aulagnier, 1997; Gewalt, 1989). Some bottlenose dolphins also create bubble rings by striking the surface of the water with their tails (Pace, 2000). One bottlenose dolphin released bubbles from her mouth while positioned vertically and upside down in the water. This dolphin flipped the bubbles once they rose to her flukes, resulting in the creation of a bubble ring (Marten et al., 1996). Other bottlenose dolphins create bubble rings by swimming on their sides, and subsequently injecting air from the blowhole into the resultant vortices (Marten et al., 1996). Finally, bottlenose dolphins also create helices by swimming in an arc while releasing bubbles, such that the bubbles fuse

into a continuous bubble spiral (Marten et al., 1996). The range of ways in which dolphins produce bubble toys is yet another indication of their behavioral flexibility and creativity.

Captive cetaceans also display creativity in the variety of ways in which they interact with their bubbles. These interactions may be as simple as observing the resultant bubbles (Delfour & Aulagnier, 1997; Pace, 2000) or as complex as swimming through the bubble rings (Gewalt, 1989; McCowan et al., 2000; Pace, 2000). Bottlenose dolphins have even been observed releasing smaller bubbles below a bubble ring resulting in the smaller bubbles traveling up and through the original ring (Kuczaj et al., 2006). Bottlenose dolphins occasionally push their bubble rings horizontally, steer them downward, or flip them through the water (Marten et al., 1996; McCowan et al., 2000; Pace, 2000).

Dolphin bubble creations are often destroyed or modified during the animal's interaction with the bubble toy. For example, Amazon River dolphins, bottlenose dolphins and beluga whales frequently bite their bubbles (Delfour & Aulagnier, 1997; Gewalt, 1989; Kuczaj & Walker, 2006; McCowan et al., 2000; Pace, 2000). Beluga whales and bottlenose dolphins are known to fluke hit their bubble creations (Delfour & Aulagnier, 1997; Kuczaj et al., 2006) and bottlenose dolphins often destroy their bubble rings by swiping them with their rostra or pectoral fins (McCowan et al., 2000). Once destroyed, captive cetaceans often interact with the remaining smaller bubbles in several ways. Beluga whales and bottlenose dolphins frequently bite or suck in the smaller bubbles (Delfour & Aulagnier, 1997; Pace, 2000), whereas bottlenose dolphins have been known to swim through the destroyed bubble toy (Pace, 2000).

Captive bottlenose dolphins sometimes modify their bubble creations. These animals have been observed to intersect bubble rings with their rostra, resulting in a smaller bubble ring being pulled from the original, larger ring. The dolphins then steer these smaller rings through the water (Marten et al., 1996). Sometimes additional air is injected into the already existing bubble ring, thus enhancing the size of the ring (Marten et al., 1996). Finally, a second bubble ring may be released below the original ring, occasionally resulting in the two rings joining (Marten et al., 1996; McCowan et al., 2000).

McCowan et al. (2000) further analyzed the creation of consecutive bubble rings by bottlenose dolphins. They documented 181 bubble ring events created by four juvenile male bottlenose dolphins. All bubble rings were rated in terms of quality, ranging from "excellent" to "poor." Consecutive bubble rings were more likely to join if the quality of the first ring was excellent. Only 27% of the 151 single bubble ring events that were of excellent quality were not followed by a second bubble ring. Moreover, 80% of the initial bubble rings produced during double bubble ring events were of excellent quality. Thus, the dolphins were more likely to produce a second bubble ring when the quality of the first bubble ring was excellent. Based on these data, the authors suggested that the dolphins were monitoring the quality of their bubble rings, and that the results of this evaluation determined the release of a second bubble ring.

***Play with other species***

Several wild and captive cetacean species interact with prey species in various ways, some of which may involve play. Wild bottlenose dolphins worldwide have been reported to interact with their prey by repeatedly tossing it into the air and hitting it with their flukes (Bel'kovich et al., 1991; Bloom, 1991; Kuczaj & Yeater, 2007; Norris & Dohl, 1980). The tucuxi have also been observed repetitively catching and releasing their prey prior to consuming it (Spinelli et al., 2002). Although this behavior has generally been labeled as play, it is possible that such manipulation of prey might prepare the fish for consumption (Norris & Dohl, 1980). Wild juvenile bottlenose dolphins at Monkey Mia, Australia chase small fish, but do not actually catch or ingest the animals (Mann & Smuts, 1999). Captive cetaceans, including harbor porpoises (*Phocoena phocoena*), common dolphins and bottlenose dolphins have also been reported to chase live fish and repetitively toss their food playfully (Defran & Pryor, 1980; Tavolga, 1966).

Interspecies play is not limited to prey items. For example, free-ranging bottlenose dolphins carry jellyfish, and rough-toothed dolphins carry puffer fish (Bel'kovich et al., 1991; Ritter, 2002; Steiner, 1995). Although these may be cases of play, these cetaceans could be using the animals for tactile stimulation given their toxic nature. Bottlenose dolphins may be aware of which fish are potentially dangerous or poisonous, as evidenced by a captive dolphin retrieving a venomous scorpionfish (*Scorpanena guttata*) and using it to chase a moray eel (*Gymnothorax mordax*) out of a crevice in its exhibit (Brown & Norris, 1956).

In captivity, dolphins interact with a variety of other species that share their habitat. This play takes the form of chasing, pushing and biting the other species. For example, Defran & Pryor (1980) reported that harbor porpoises played with sea stars encountered in their tanks. Common dolphins and bottlenose dolphins sometimes shake and pull sharks around by their tails (Bel'kovich et al., 1970; Defran & Pryor, 1980; McBride & Hebb, 1948). Bottlenose dolphins also intercept sea turtles that are approaching the surface to breathe and then push them to the bottom of the pool (Tayler & Saayman, 1973). Finally, Tavolga (1966) documented bottlenose dolphins chasing live fish in their exhibits without consuming them, working cooperatively to remove fish from habitat decor, and using feeder fish to bait larger fish from crevices.

Birds appear to be attractive play objects for both wild and captive cetaceans. Wild dusky dolphins repeatedly pulled kelp gulls (*Larus dominicanus*) and hooded gulls (*Larus maculipennis*) 30 to 60 cm underwater (Würsig, 2002) without consuming them, a possible form of play. A pilot whale (*Globicephala mela*) repetitively surfaced in the middle of a large flock of floating Common Eiders (*Somateria mollissima*), resulting in the scattering of the alarmed birds (Heubeck, 2001). Mann and Smuts (1999) documented a 22 day-old bottlenose dolphin calf poking a cormorant with its rostrum several times in Monkey Mia, Australia. A loon (*Gavia iixmer*) was the object of attention as it was pushed and tossed about by an adult bottlenose dolphin in Florida (Hewitt, 1986). Other instances of birds as potential play items include captive bottlenose dolphins

nipping at floating pelicans (McBride & Hebb, 1948), bottlenose dolphins playing with seagulls (Bel'kovich et al.,1991), and captive killer whales baiting seagulls with fish to lure them close enough to catch (Kuczaj, Lacinak, Garver, & Scarpuzzi, 1998; Kuczaj & Makecha, 2008).

Harassing play activities are not limited to birds. Tayler & Saayman (1973) reported a group of approximately 20 bottlenose dolphins herding a group of Cape fur seals (*Arctocephalus pusillus*) in Plettenberg Bay, Africa. The dolphins changed their direction of travel and encircled eight of the resting seals. The dolphins subsequently herded these individuals for about 40 minutes over a distance of two km. The dolphins did not harm the seals and were later seen foraging. Although the behavior of the dolphins was similar to that seen when herding fish, the behavior appeared to be a form of play.

An analogous incident was reported by Weller et al. (1996). In this case several short-finned pilot whales (*Globicephala macrorhynchus*) encircled a group of sperm whales. The sperm whales appeared to be alarmed by this behavior. However, because short-finned pilot whales do not prey upon sperm whales, the authors suggested that the behavior of the pilot whales was play.

Apparent play bouts do not always end benignly. Interactions between bottlenose dolphins and harbor porpoises in Scotland have often resulted in the death of the target species. These bottlenose dolphins were reported to be responsible for the deaths of 42 harbor porpoises between 1991 and 1993 (Ross & Wilson, 1996). Similarly, about 74 harbor porpoises have been found along California beaches during the past year (KTVU.com, 2009). Both populations of bottlenose dolphins were observed repeatedly chasing, fluke-hitting, and tossing the harbor porpoises, and post-mortem examinations of the resulting wounds indicated that the activities of the dolphins were to blame for the mortalities. Given that these two species do not compete for resources, it has been suggested that the behavior displayed by the bottlenose dolphins was a form of play (Ross & Wilson, 1996). However, competition for females has been implicated as an alternative cause for this behavior (KTVU.com, 2009).

Humans can also be objects of play for wild and captive cetaceans. Wild cetaceans often solicit human attention for provisioning, cooperative hunting purposes and possible social needs (for a review see Lockyer, 1990). The bottlenose dolphins at Monkey Mia, Australia engage humans in games that involve passing seagrass between the human and dolphin participants (Mann & Smuts, 1999). Captive cetaceans also involve humans in their object play as well (Brown & Norris, 1956; Caldwell & Caldwell, 1972; Kuczaj et al., 2006). Captive bottlenose dolphins were often observed playing "ball toss" with human observers at a marine aquarium in Southern Mississippi (Trone et al., 2005). However, bottlenose dolphins have also been known to harass humans by pulling on diving or cleaning equipment (Tavolga, 1966), or even pulling people into the water that are standing near their pools (Bel'kovich et al., 1970). It is not clear if such behavior is play or aggressive, particularly since some dolphin play results in the injury or death of their animate play objects (Kuczaj & Makecha, 2008).

**Table 1**
*List of wild and captive cetacean species and play item.*

| Cetacean Species | Play Item/Activity | Wild or Captive | Reference |
|---|---|---|---|
| Amazon River dolphin | bubbles | captive | Gewalt, 1989 |
| Amazon River dolphin | pool cleaning equipment | captive | Gewalt, 1989 |
| Amazon River dolphin | prey items | wild | Spinelli et al., 2002 |
| Amazon River dolphin | seaweed | wild | Spinelli et al., 2002 |
| Atlantic spotted dolphin | bubbles | wild | Marten et al., 1996 |
| Atlantic spotted dolphin | seagrass | wild | Miles & Herzing, 2003 |
| beluga whale | bubbles | captive | Delfour & Aulagnier, 1997 |
| beluga whale | bubbles | wild | Marten et al., 1996 |
| bottlenose dolphin | bandages | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | beaching | captive | DeLong, 1999; Kuczaj et al., 2006 |
| bottlenose dolphin | buckets | captive | Kuczaj et al., 2006 |
| bottlenose dolphin | buoys | captive | Kuczaj et al., 2006 |
| bottlenose dolphin | coins | captive | Caldwell & Caldwell, 1972 |
| bottlenose dolphin | feather | captive | Brown & Norris, 1956; Kuczaj et al., 2006; Tavolga, 1966 |
| bottlenose dolphin | fish | captive | Brown & Norris, 1956; Defran & Pryor, 1980; McBride & Hebb, 1947; Tavolga, 1966 |
| bottlenose dolphin | gauze | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | hat | captive | Tavolga, 1966 |
| bottlenose dolphin | knotted ropes | captive | Kuczaj et al., 2006 |
| bottlenose dolphin | pelican | captive | McBride & Hebb, 1947 |
| bottlenose dolphin | pieces of wood | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | plastic bat | captive | Kuczaj et al., 2006 |
| bottlenose dolphin | plastic foam | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | pool cleaning equipment | captive | Tayler & Saayman, 1973 |
| bottlenose dolphin | prey items | captive | Tavolga, 1966 |

**Table 1 (cont.)**

| | | | |
|---|---|---|---|
| bottlenose dolphin | rope | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | scarves | captive | Kuczaj et al., 2006; Tavolga, 1966 |
| bottlenose dolphin | sea gull | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | sea turtle | captive | Defran & Pryor, 1980; McBride & Hebb, 1947; Tayler & Saayman, 1973 |
| bottlenose dolphin | shark | captive | Bel'kovich et al., 1970; Brown & Norris, 1956; McBride & Hebb, 1947 |
| bottlenose dolphin | skate/ray | captive | Bel'kovich et al., 1970; Brown & Norris, 1956 |
| bottlenose dolphin | sunglasses | captive | Kuczaj et al., 2006 |
| bottlenose dolphin | tape | captive | Bel'kovich et al., 1970 |
| bottlenose dolphin | eel | captive | Brown & Norris, 1956; Defran & Pryor, 1980 |
| bottlenose dolphin | sea lion | captive | Defran & Pryor, 1980 |
| bottlenose dolphin | baleen whale | wild | Würsig, 2002 |
| bottlenose dolphin | jellyfish | wild | Bel'kovich et al., 1991 |
| bottlenose dolphin | loon | wild | Hewitt, 1986 |
| bottlenose dolphin | prey items | wild | Bel'kovich et al., 1991; Bloom, 1991; Mann & Smuts, 1999; Norris & Dohl, 1980 |
| bottlenose dolphin | seaweed | wild | Bloom 1991; Würsig & Würsig, 1979 |
| bottlenose dolphin | sperm whale | wild | Würsig, 2002 |
| bottlenose dolphin | Cape fur seal | wild | Tayler & Saayman, 1973 |
| bottlenose dolphin | ball | captive | Bel'kovich et al., 1970; Brown & Norris, 1956; Kuczaj et al., 2002, 2006; Norris & Dohl, 1980 |
| bottlenose dolphin | bubbles | captive | Kuczaj et al., 2006; McCowan et al., 2000; Pace, 2000; Tizzi et al., 2001 |

**Table 1 (cont.)**

| | | | |
|---|---|---|---|
| bottlenose dolphin | wallet | captive | Tavolga, 1966 |
| bottlenose dolphin | cormorant | wild | Mann & Smuts, 1999 |
| bottlenose dolphin | harbor porpoise | wild | Ross & Wilson, 1996 |
| bowhead whale | log | wild | Würsig et al., 1989 |
| common dolphin | prey items | captive | Defran & Pryor, 1980; Tavolga, 1966 |
| dolphin (unspecified sp.) | penguin | wild | Würsig, 2002 |
| dusky dolphin | sea gull | wild | Würsig, 2002 |
| dusky dolphin | South American sea lion | wild | Würsig & Würsig, 1980 |
| dusky dolphin | Southern right whale | wild | Würsig & Würsig, 1980 |
| dusky dolphin | seaweed | wild | Würsig, 2002; Würsig & Würsig, 1980 |
| false killer whale | ball | captive | Kuczaj et al., 2002 |
| harbor porpoise | seastar | captive | Defran & Pryor, 1980 |
| harbor porpoise | prey items | captive | Defran & Pryor, 1980 |
| Hawaiian spinner dolphin | towel | captive | Prescott, 1968, as cited in Caldwell & Caldwell, 1972 |
| Hector's dolphin | seagrass | wild | Slooten & Dawson, 1994 |
| killer whale | ball | captive | Kuczaj et al., 2002 |
| killer whale | beaching | wild | Guinet, 1991 |
| Pacific spotted dolphin | bubbles | wild | Marten et al., 1996 |
| Pacific white-sided dolphin | feather | captive | Brown & Norris, 1956 |
| pilot whale | common eider | wild | Heubeck, 2001 |
| rough-toothed dolphin | plastic bag | wild | Kuczaj & Highfill, 2005; Kuczaj & Yeater, 2007 |
| rough-toothed dolphin | prey items | wild | Kuczaj & Yeater, 2007 |
| rough-toothed dolphin | seagrass | wild | Kuczaj & Yeater, 2007 |
| rough-toothed dolphin | seaweed | wild | Kuczaj & Yeater, 2007 |
| short-finned pilot whale | sperm whale | wild | Weller et al., 1996 |

## Conclusion

Play is notoriously difficult to define. Part of the problem is that play behaviors occur in contexts other than play, including foraging, mating, and social negotiation (specifically those to determine social ranking). Although difficult to define, several functions of play have been postulated (Bekoff & Byers, 1981; Coelho & Bramblett, 1982; Colvin & Tissler, 1985; Connor et al., 2000; Guinet, 1991; Kuczaj et al., 2006; Kuczaj & Makecha, 2008; Kuczaj & Trone, 2001; Miller & Nadler, 1982; Rose, 1992; Thompson, 1996; Walters, 1987; West, 1974). These functions include: providing a way of helping animals gain knowledge of objects or of their environment, providing a mechanism by which young animals may perfect motor skills through the use of practice, facilitation of the development of flexible problem solving skills by providing a non-threatening context in which animals can explore the consequences of new behaviors, and providing young animals a venue in which they can cultivate important social relationships. The wide body of research reviewed here provides several examples of each of these theorized functions.

The study of play in cetaceans is made even more difficult due to the nature of the environment in which they live. For the most part, observations of wild cetaceans are limited to surface behaviors, although there are exceptions (e.g., Dudzinski, 1998; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Dudzinski et al., 2003; Herzing, 1996, 2005; Herzing & Johnson, 1997; Herzing, Moewe, & Brunnick, 2003). It is also difficult to maintain a sustained study on wild cetaceans due to the difficulty inherent in following the animals or observing a specific animal on multiple occasions. Studies of captive cetaceans can provide insight into the long-term development of play behavior as well as enable consistent monitoring of individual and group activity because following and re-sighting in captive contexts is relatively easy.

This review has illustrated the significance of both wild and captive studies of cetacean play. Complementary data obtained from both population types make it easier to understand the extent, functions, and underlying psychological mechanisms of cetacean play. Investigations of wild cetaceans are invaluable in that they provide unique insights concerning the extent of cetacean play. Studies of captive populations can provide detailed information about ontogeny and cultural transmission of play behaviors. Thus, pooling the results obtained from both wild and captive studies leads to more robust theories, conclusions and understanding of play, and is likely true for many areas of cetacean behavior.

As illustrated in this review, it is clear that play is an important component of life for cetaceans. As a result of these studies of play, our breadth of knowledge regarding the social dynamics, developmental processes, communicative flexibility and cognitive abilities of cetaceans has been expanded. With applications ranging from conservation biology to husbandry, the study of play among wild and captive animals should continue to provide insight into the complex world of these denizens of the sea.

## References


Bekoff, M., & Allen, C. (1998). *Animal play: Evolutionary, comparative, and ecological perspectives*. Cambridge, UK: Cambridge University Press.

Bekoff, M., & Byers, J. (1981). A critical reanalysis of the ontogeny of mammalian social and locomotor play: An ethological hornet's nest. In W. Barlow, K. Immelman, & L. Petrinovich (Eds.), *Behavioural development: The bielefield interdisciplinary project* (pp. 296-337). New York: Cambridge University Press.

Bel'kovich, V. M., Ivanova, E. E., Kozarovitsky, L. B., Novikova, E. V., & Kharitonov, S. P. (1991). Dolphin play behavior in the open sea. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 67-77). Los Angeles: University of California Press.

Bel'kovich, V. M., Krushinskaya, N. L., & Gurevich, V. S. (1970). *The behavior of dolphins in captivity*. No. 50701. Washington, DC: Joint Publications Research Service.

Bloom, P. (1991). The diary of a wild, solitary, bottlenose dolphin (*Tursiops truncatus*), resident off Amble on the north Northumberland coast of England, from April 1987 to January 1991. *Aquatic Mammals, 17*, 103-119.

Bornstein, M. H., & O'Reilly, A. W. (1993). *The role of play in the development of thought*. San Francisco, CA: Jossey-Bass Publishers.

Brown, D. H., & Norris, K. S. (1956). Observations of captive and wild cetaceans. *Journal of Mammalogy, 37*(3), 311-326.

Bruner, J. S. (1972). Nature and use of immaturity. *American Psychologist, 27*, 687-708.

Bruner, J. S. (1973). Organization of early skilled action. *Child Development, 44*, 1-11.

Burghardt, G. M. (2005). *The genesis of animal play*. Cambridge, MA: MIT Press.

Caldwell, M. C., & Caldwell, D. K. (1972). Behavior of marine mammals. In S. Ridgway (Ed.), *Mammals of the sea: Biology and medicine* (pp. 419-465). Springfield, IL: Charles C Thomas Publisher.

Caldwell, D. K., & Fields, H. M. (1959). Surf-riding by Atlantic bottle-nosed dolphins. *Journal of Mammalogy, 40*, 454-455.

Caro, T. M. (1995). Short-term costs and correlates of play in cheetahs. *Animal Behaviour, 49*, 333-345.

Coelho, A. M., & Bramblett, C. A. (1982). Social play in differentially reared infant and juvenile baboons (*Papio* e.). *American Journal of Primatology, 3*, 153-160.

Colvin, J. D., & Tissler, G. (1985). Affiliation and reciprocity in sibling and peer relationships among free-ranging immature male rhesus monkeys. *Animal Behaviour, 33*, 959-977.

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

Defran, R. H., & Pryor, K. (1980). The behavior and training of cetaceans in captivity. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 319-362). Malabar, FL: Krieger Publishing Company.

Delfour, F., & Aulagnier, S. (1997). Bubbleblow in beluga whales (*Delphinapterus leucas*): A play activity? *Behavioural Processes, 40*, 183-186.

DeLong, T. C. (1999). Observations of free-play behavior in captive juvenile bottlenose dolphins (*Tursiops truncatus*). In S. Reifel (Ed.), *Play and culture studies, Vol. 2: Play contexts revisited* (pp. 219-238). Stamford, CT: Ablex Publishing Corporation.

Dudzinski, K. M. (1998). Contact behavior and signal exchange among Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals, 24*(3), 129-142.

Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj, S. A. (2009). Flipper's flipper – a comparison of how, where and why spotted and bottlenose dolphins use their pectoral fins to touch peers. *Behavioural Processes, 80*, 182-190.

Dudzinski, K. M., Sakai, M., Masaki, K., Kogi, K., Hishii, T., & Kurimoto, M. (2003). Behavioral observations of adult and sub-adult dolphins towards two dead bottlenose dolphins (one female and one male). *Aquatic Mammals, 29*(1), 108-116.

Finneran, J. J., Oliver, C. W., Schaefer, K. M., & Ridgway, S. H. (2000). Source levels and estimated yellowfin tuna (*Thunnus albacares*) detection ranges for dolphin jaw pops, breaches, and tail slaps. *Journal of the Acoustical Society of America, 107*, 649-656.

Fagan, R. (1981). *Animal play behavior*. New York: Oxford University Press.

Fagen, R. (1993). Primate juveniles and primate play. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 182-196). Oxford, UK: Oxford University Press.

Ficken, M. S. (1977). Avian play. *Auk, 94***,** 573-582.

Garvey, C. (1974). Some properties of social play. *Merrill-Palmer Quarterly, 20*, 163-180.

Gewalt, W. (1989). Orinoco freshwater dolphins (*Inia geoffrensis*) using self-produced air bubble rings as toys. *Aquatic Mammals, 15*(2), 73-79.

Groos, K. (1898). *The play of animals*. New York: Appleton & Company.

Guinet, C. (1991). Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology, 69*, 2712-2716.

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology, 73*, 27-33.

Hanson, M. T., & Defran, R. H. (1993). The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquatic Mammals, 19*(3), 127-142.

Harcourt, R. (1991). The development of play in the South American fur seal. *Ethology, 88*, 191-202.

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals, 22*(2), 61-79.

Herzing, D. L. (2005). Transmission mechanisms of social learning in dolphins:underwater observations of free-ranging dolphins in the Bahamas. Autour de L'Ethologie et de la Cognition Animale. Presses Universitaires de Lyon.

Herzing D. L., & Johnson, C. M. (1997) Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals, 23*(2), 85-99.

Herzing, D. L, Moewe, K. & B. J. Brunnick (2003). Interspecies interactions between Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, on Grerat Bahama Bank, Bahamas. *Aquatic Mammal, 29*(3), 335-341

Heubeck, M. (2001). Pilot whale apparently playing with moulting common eiders. *Scottish Birds, 22*(1), 62.

Hewitt, O. H. (1986). Dolphin interferes with loon. *Florida Field Naturalist, 14*, 100.

KTVU.com. (2009, November 6). *Mysterious porpoise deaths blamed on berserk dolphins: Deadly attack on lone porpoise caught on camera*. Retrieved November 10, 2009, from: KTVU.com website: http://www.ktvu.com/news/21543657/detail.html?taf=fran

Kuczaj, S. A., & Highfill, L. E. (2005). Dolphin play: Evidence for cooperation and culture? *Behavioral and Brain Sciences, 28*(5), 705-706.

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

Kuczaj, S. A. II, Lacinak, C. T., Garver, A., & Scarpuzzi, M. (1998). Can animals enrich their own environment? In V. J. Hare & K. E. Worley (Eds.) *Proceedings of the Third International Conference on Environmental Enrichment* (pp. 168-170), Orlando, FL. San Diego, CA.: The Shape of Enrichment.

Kuczaj, S. A., & Makecha, R. (2008). The role of play in the evolution and ontogeny of contextually flexible communication. In D. K. Oller & U. Griebel (Eds.), *Evolution of communicative flexibility: Complexity, creativity, and adaptability in human and animal communication* (pp. 253-277). Cambridge, MA: The MIT Press.

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

Kuczaj, S. & Trone, M. (2001). Why do dolphins and whales make their play more difficult? *Genetic Epistemologist, 29*, 57.

Kuczaj, S. A., & Walker, R. T. (2006). How do dolphins solve problems? In E. A. Wasserman & T. R. Zentall (Eds.), *Comparative cognition* (pp. 580-601). Oxford: Oxford University Press.

Kuczaj, S. A. II., & Yeater, D. B. (2007). Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *Journal of the Marine Biological Association of the United Kingdom, 87*, 141–148.

Kuyk, K., Dazey, J., & Erwin, J. (1976). Play patterns of pigtail monkey infants: Effects of age and peer presence. *Journal of Biological Psychology, 18*, 20-23.

Kyngdon, D. J., Minot, E. O., & Stafford, K. J. (2003). Behavioural responses of captive common dolphins *Delphinus delphis* to a 'Swim-with-Dolphin' programme. *Applied Animal Behaviour Science, 81*, 163–170.

Lockyer, C. (1990). Review of incidents involving wild, sociable dolphins, worldwide. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 337-353). San Diego, CA: Academic Press.

Lusseau, D. (2006). Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand. *Behavioural Processes, 73*, 257-265.

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

Markus, N., & Croft, D. B. (1995). Play behavior and its effects on social development of common chimpanzees (*Pan troglodytes*). *Primates, 36*, 213-225.

Martin, A. R., da Silva, V. M. F., & Rothery, P. (2008). Object carrying as socio-sexual display in an aquatic mammal. *Biology Letters, 4*, 243-245. doi:10.1098/rsbl.2008.0067

Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996, August). Ring bubbles of dolphins. *Scientific American*, 275, 83-87.

McBride, A.F., & Hebb, D. O. (1948). Behavior of the captive bottlenose dolphin, *Tursiops truncatus*. *Journal of Comparative Physiological Psychology, 41*, 111-123.

McCowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): Implications for cognition. *Journal of Comparative Psychology, 114*(1), 98-106.

Miles, J. A., & Herzing, D. L. (2003). Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquatic Mammals, 29*, 363-377.

Miller, L. C., & Nadler, R. D. (1982). Mother-infant relations and infant development in captive chimpanzees and orangutans. *International Journal of Primatology, 2*, 247-261.

Muller-Schwarze, D., Stagge, B., & Muller-Schwarze, C. (1982). Play behaviour: Persistence, decrease and energetic compensation during food shortage in deer fawns. *Science, 215*, 85-87.

Norris, K. S., & Dohl, T. P. (1980). The structure and functions of cetacean schools. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 211-261). Malabar, FL: Krieger Publishing Company.

Ortega, J. C., & Beckoff, M. (1987). Avian play: Comparative evolutionary and developmental trends. *Auk, 104*, 338-341.

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

Parra, G. J. (2007). Observations of an Indo-Pacific humpback dolphin carrying a sponge: object play or tool use? *Mammalia, 71*(3), 147-149.

Parten, M. B. (1932). Social participation among preschool children. *Journal of Abnormal and Social Psychology, 27*, 243-269.

Payne, R. (1995). *Among whales*. New York: Charles Scribbner's Sons.

Piaget, J. (1951). *Plays, dreams, and imitation in childhood*. New York: Norton.

Piaget, J. (1952). *The origins of intelligence in children*. New York: Norton.

Power, T.G. (2000). *Play and exploration in children and animals.* Mahwah, NJ: Erlbaum.

Ritter, F. (2002). Behavioral observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995–2000), with special reference to their interactions with humans. *Aquatic Mammals, 28*, 46–59.

Rose, N. A. (1992). The social dynamics of male killer whale, *Orcinus orca*, in Johnstone Strait, British Columbia. Ph.D. Thesis, University of California, Santa Cruz.

Ross, H. M., & Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society B: Biological Sciences, 263*, 283-286.

Saayman, G. S., & Tayler, C. K. (1973). Social organization of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. *Journal of Mammalogy, 54*(4), 993-996.

Saayman, G. S., Tayler, C. K., & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus*, Ehrenburg). *Behaviour, 44*, 212-233.

Slooten, E. (1994). Behavior of Hector's dolphin: Classifying behavior by sequence analysis. *Journal of Mammalogy, 75*(4), 956-964.

Slooten, E., & Dawson, S. M. (1994). Hector's dolphins. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of Marine Mammals* (pp. 311-334). London: Academic Press.

Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (*Delphinidae, Tursiops* sp.): A foraging specialization involving tool use? *Ethology 103*, 454– 465.

Sommer, V., & Mendoza-Granados, D. (1995). Play as indicator of habitat quality: A field study of langur monkeys (*Presbytis entellus*). *Ethology, 99*, 177-192.

Spinelli, L. H. P., Nascimento, L. F., Yamamoto, M. E. (2002). Identification and description of play in a scarcely studied species, the tucuxi (*Sotalia fluviatilis*) in a field site. *Estudos de Psicologia, 7*(1), 165-171.

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology*, *76*, 141-168.

Steiner, L. (1995). Rough-toothed dolphin, *Steno bredanensis*: A new species record for the Azores, with some notes on behaviour. *Arquipélago*, *13A*, 125–127.

Sylvestre, J. P. (1985). Some observations on behaviour of two Orinoco dolphins (*Inia geoffrensis*). *Aquatic Mammals*, *11*(2), 58-65.

Tavolga, M .C. (1966). Behavior of the bottlenose dolphin (*Tursiops truncatus*): Social interactions in a captive colony. In K .S. Norris (Ed.), *Whales, dolphins, and porpoises* (pp. 718-730). Berkeley, CA: University of California Press.

Tayler, C. K., & Saayman, G. S. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, *44*, 286-298.

Thomas, P. O., & Taber, S. M. (1984). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, *88*(1/2), 42-60.

Thompson, K. V. (1996). Behavioral development and play. In D. Kleiman, M. E. Allen, K.V. Thompson, & S. Lumpkin (Eds.), *Wild Mammals in Captivity: Principles and Techniques* (pp. 352-371). Chicago: University of Chicago Press.

Tizzi, R., Castellano, A., & Pace, D. S. (2001). The development of play behavior in a in calf (*Tursiops truncatus*). In P. G. H. Evans, R. Pitt-Aiken, & E. Rogan (Eds.), *Proceedings of the Fourteenth Annual Conference of the European Cetacean Society*, (pp. 152-157), Cork, Ireland.

Trone, M., Kuczaj, S., & Solangi, M. (2005). Does participation in dolphin–human interaction programs affect bottlenose dolphin behaviour? *Applied Animal Behaviour Science*, *93*, 363–374

Vanderberg, B. (1978). Play and development from an ethological perspective. *American Psychologist*, *33*, 724-738.

Veasey, J. S., Waran, N. K., & Young, R .J. (1996). On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare*, *5*(2), 139-153.

Walters, J. R. (1987). Transition to adulthood. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 358-369). Chicago: University of Chicago Press.

Weller, D. W., Würsig, B., Whitehead, H., Norris, J. C., Lynn, S. K., Davis, R. W., et al.. (1996). Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. *Marine Mammal Science*, *12*, 588-594.

West, M. (1974). Social play in the domestic cat. *American Zoologist*, *14*, 427-436.

Würsig, B. (2002). Playful behavior. In W. F. Perrin, B. Wursig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 942-945). San Diego, CA: Academic Press.

Würsig, B., Dorsey, E. M., Richardson, W. J., & Wells, R. S. (1989). Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. *Aquatic Mammals*, *15*(1), 27-37.

Würsig, B., & Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the south Atlantic. *Fishery Bulletin*, *77*(2), 399-412.

Würsig, B., & Würsig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the south Atlantic. *Fishery Bulletin*, *77*(4), 871-890.