Learn Behav (2017) 45:335–354
DOI 10.3758/s13420-017-0291-0

Learning to play: A review and theoretical investigation of the developmental mechanisms and functions of cetacean play

Heather M. Hill[1] · **Sarah Dietrich**[2] · **Briana Cappiello**[3]

Published online: 4 August 2017

Abstract Play is a behavioral phenomenon most commonly observed in the young of both solitary and social species. Documentation of play in cetaceans varies across species and settings. Cetacean play behavioral repertoires include a broad range of actions, such as the manipulation of diverse objects, blowing bubbles, chasing conspecifics, and swimming in spirals through the water. As is common in research on animal play, cetacean play has been grouped into categories by its form, including locomotor play, object play, and different variations of social play, such as affiliative games, play fighting, and socio-sexual play. Research has primarily focused on recording the topography of cetacean play and the demographics of the individuals engaging in play. However, these classifications are insufficient to address the possible developmental and societal functions of cetacean play behaviors, or the mechanisms with which play behaviors are spread between conspecifics and acquired by young members of cetacean populations. This article applies several developmental and social learning theories in order to organize current knowledge and guide future research.

Keywords Cetacean · Social learning · Development · Play

✉ Heather M. Hill
hhill1@stmarytx.edu

[1] St. Mary's University, San Antonio, TX, USA

[2] University at Buffalo, State University of New York, Buffalo, NY, USA

[3] The University of Southern Mississippi, Hattiesburg, MS, USA

Cetaceans are often stereotyped as playful. Their aerial and wave surfing behaviors are viewed by tourists as joyful displays, and the dolphin's jawline gives the distinct impression of a fixed smile. Fagen (1981) included descriptions of cetaceans leaping into the air and twisting their bodies in his seminal book *Animal Play Behavior*. At the time, Fagen considered the contribution of cetacean play research as broadening the understanding of play beyond the "implicit assumptions of quadrupedalism" (p. 137). Since play was recognized by Fagen as a legitimate scientific topic, we now know that play of some form has been observed in all major taxa—mammals, avians, reptiles, invertebrates, and amphibians (Burghardt, 2005). However, not all taxa appear to engage in more complex forms of play, such as object play and social play. Beyond the notion that cetacean play is significant because it occurs without hind limbs, we now recognize that the levels of sophisticated social reasoning and cognitive functioning among cetaceans correspond to other animals that engage in complex forms of play (e.g., corvids: Osvath & Sima, 2014; primates: Palagi et al., 2016).

The purpose of this article is to examine the extant body of literature on cetacean play within the theoretical frameworks of developmental psychology and social learning. Most cetacean play research to date has been based on inductive reasoning, following a bottom-up approach. To reflect the development of this field, the article is divided in three major sections: (1) foundational descriptive knowledge of play, with an emphasis on cetacean play; (2) an examination of proposed functions of play through the lenses of several theories: Groos's practice theory of play, Piaget's cognitive developmental theory, Parten's stages of social play, and two hierarchical organization schemes, proposed separately by Fagen and Mitchell (summarized in Table 1); and finally, (3) possible transmission mechanisms of play. Specific questions that guided this review and the proposed organizational scheme of cetacean play included:

Table 1 Brief overview of key theories

Theory	Relevant Highlights
Theories of Development (Based on Human Research)	
Groos, 1898; 1901	• Immaturity at birth and a prolonged period of maturation are considered advantageous as they allow for development through play. • The function of play is described as developing instinctual capacities to maturity and then learning noninstinctual skills.
Piaget, 1951	• Development is modeled as sequential stages with play reflecting cognitive-developmental changes at each stage. • During the early sensorimotor stage (0–2 years for humans), play progresses from early preoccupation with body movements, sensory experiences, and how actions can influence the environment.
Parten, 1932	• Children are thought to progress through six sequential levels of play characterized by increasing levels of social participation: unoccupied behavior, solitary play, onlooker behavior, parallel play, associative play, and then cooperative play. • Stages are believed to increase in complexity with social participation/cooperative play being the most mature level of peer interaction.
Classification Systems of Animal Play	
Fagen, 1995	• Descriptive approach to classifying play as it progresses from noninteractive, repeated actions to more complex play that involves s ocial interactions of different forms. • Advanced play includes "games" with others as well as more complex forms of solitary locomotor and object play.
Mitchell, 1990	• Hierarchical classification system for play that progresses from basic locomotor actions to complex forms of play including pretense and cooperative imaginative play.

- Does cetacean play progress through stages of play or meet age-dependent milestones?
- What are the functions of play for adult and juvenile cetaceans?
- How does play function within cetacean societies?
- Of the following transmission mechanisms, which ones can account for the current data on play behavior and development in cetaceans: independent learning or social learning, including stimulus enhancement; behavioral contagion; imitation; or teaching?

By considering the available data through these theoretical lenses, we may better understand play for its role in the physical, cognitive, emotional, and social development of cetaceans at the individual and group levels.

Characterizing play: What we know

The problem of identifying play in cetaceans

Chasing, wave riding, aerials, and object manipulation were classified by early researchers as cetacean play and are still some of the most frequently reported play behaviors. However, even these prototypical play behaviors also appear in nonplayful functional contexts, which can be misinterpreted as playful by naïve viewers (Janik, 2015). For example, aerial behaviors are more nuanced than they were originally described and are composed of different classes: spy hopping (bobbing the head above water), slaps (tail, fluke, head, side, and back slaps caused by bringing the body part out of the water then quickly hitting the water's surface), leaps, breaches, flips, and pinwheels (Norris, Wursig, & Wells, 1994; Paulos, Trone, & Kuczaj, 2010; Whitehead, 1985). Some high-speed chases and aerial leaping are indicative of serious fighting, and leaps during high-speed swimming may be either a more efficient means of travel than swimming underwater or an artifact associated with quickly surfacing to breathe. Similarly, body slaps may be performed to remove parasites or to communicate through both the action and the sound produced rather than solely for the sake of play (Janik, 2015; Whitehead, 1985).

Defining play

The problem of identifying, and even defining, play is not unique to cetaceans; it is a burden carried by the entire field of research on animal play (Burghardt, 2005). Occasionally, research on cetacean play has avoided the definitional debate by working on the premise that people "are adept at recognizing play when we see it" but are "exceptionally inexpert at defining the term" (Paulos et al., 2010, p. 701). At other times, researchers have worked off of the original definitions of play proposed by Fagen (1981). As defined by Fagen (1981), play behaviors should be intrinsically rewarding and appear pleasurable to the player, voluntary, and spontaneous (not driven by extrinsic goals or biological consequence). Given that play behaviors share some characteristics of nonplay behaviors, play behaviors must be discriminated from the species-typical, appropriate contextual actions. Thus, play behaviors tend to be species-typical behaviors that are performed out of context, triggered by different stimuli, directed toward substitute objects, or modified in structure. Modifications can include exaggerated, reordered, incomplete, brief, varied in sequence, and inhibited forms of the typical behavior. Play also often occurs in a supportive or benign environment, such that the player is not threatened or hungry (but see Blois-Heulin et al., 2015; Hausberger, Fureix, Bourjade, Wessel-Robert, & Richard-Yris, 2012). More recently, Burghardt (2005) reimagined the

definition of play to include many of these different characteristics into one definition of play involving five criteria: (1) play is not fully functional, and therefore does not contribute to the immediate survival of the individual; (2) play is spontaneous yet intentional, pleasurable, or rewarding; (3) play represents a modification of an inherent behavior, such as in its form, timing, sequence, or target; (4) play is often repeated but not rigid, as in stereotypies; and (5) play occurs when in a "relaxed field" (Burghardt, 2005, p. 81) and not during other behavioral states, such as foraging, breeding, or defense.

Indicators of a relaxed field or a positive mood have different expressions that may not always be observable (Burghardt, 2005). For example, humans and primates utilize facial indicators such as "smiles" or "play faces," canines use "play bows," mongooses emit specific sounds during play bouts with others, and other animals may use chemical communication signals to indicate a state of relaxation (reviewed by Burghardt, 2005). Unfortunately, the facial indicators of positive affect familiar to humans and primates are not possible given the anatomy of cetaceans. Although cetaceans like dolphins and belugas (*Delphinapterus leucas*) appear to look "happy" due to their morphology, it is especially difficult to connect observable behavior to a playful mood in cetaceans, because high-energy behaviors such as leaps, breaches, and spins, or high-arousal responses, such as vocalizations, are often used functionally in their daily activities (Lusseau, 2006; Pearson, 2017; Würsig & Würsig, 1980). Identifying positive affect in cetaceans can be quite challenging but is not impossible (e.g., de Vere & Kuczaj, 2016; Dibble, Van Alstyne, & Ridgway, 2016; Kuczaj & Horback, 2012).

Signals for identifying play

One way to distinguish between functional behaviors and play behaviors is through the expression of play signals. Such signals may include unambiguous behaviors, referencing gestures, and acoustics that indicate that actions are playful (Bender, 2012; Burghardt, 2005; Kuczaj & Horback, 2012; Palagi et al., 2016). Utilizing play signals reduces the chances of play escalating into aggression, since many play behaviors translate to functional contexts and can be misinterpreted (Burghardt, 2005; Kuczaj & Horback, 2012; Palagi et al., 2016). Play signals by cetaceans represent an understudied and recent area of research. Kuczaj and Makecha (2008) observed immature dolphins temporarily immobilizing themselves at the water surface during social-play bouts, which was interpreted as a possible play signal to "come push me." Bender suggested that tail request behaviors are used to pass seaweed from the tail of one dolphin to another following behind. Similarly, seaweed-dropping behaviors may also be considered play signals, since these actions solicit play by providing others the opportunity to receive or pick up seaweed to continue play. Although these behaviors have not yet been observed in wild populations, it would not be surprising if similar play signals occurred in the wild, since the requirements for successful social play are still relevant (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006).

Broad categories of play across cetaceans

Cetacean researchers tend to focus on identifying and cataloging specific types of play rather than on defining play as a broad category. Play in cetaceans is most often classified into one of three types, along the commonly used taxonomy in animal play research: (1) locomotor, (2) object, and (3) social (Burghardt, 2005; Fagen, 1981).

Locomotor play

Locomotor play has been observed in species of animals that show no other form of play, and locomotor-rotational play (body movements while an animal is otherwise stationary) is often the first play behavior exhibited by young animals (Burghardt, 2005). Since locomotor play is ubiquitous among taxa, it is not surprising that it has been observed in cetaceans. Some locomotor play in cetaceans is easily observed from the water's surface. Locomotor play can include aerial displays, such as breaches, leaps, lunges, flips, pinwheels, and various body slaps (Paulos et al., 2010; Whitehead, 1985), or underwater actions, such as swimming unpredictably or spiraling through the water. Discussed by Paulos and colleagues, southern right whales (*Eubalaena australis*) between 30 and 63 days of life exhibited aerial and other locomotor behaviors, including breaches, pectoral slaps, fluke slaps, and erratic swimming, that were categorized as play. Various species of whales and dolphins have also delighted tourists by surfing along the wake produced by boats (Baird, 2000), and in some cases dolphins have even been observed surfing the pressure waves created by larger whales (Paulos et al., 2010). Similarly, dolphins in managed care (Paulos et al., 2010), killer whales (*Orcinus orca*), and belugas have also been observed using toys to create pressure waves on which they can surf (unpublished observations, H. Hill). Cetaceans may also self-strand during play (i.e., beaching), such that an animal beaches itself by boosting its body partially out of the water and onto a beach, sloped, or flat surface. Cetaceans in both their natural habitats and managed care have been observed engaging in intentional stranding play (Guarino, Hill, & Sigman, 2016; Guinet, 1991; Guinet & Bouvier, 1995; Hill, 2009; Hill & Ramirez, 2014; Paulos et al., 2010). Bottlenose dolphins (*Tursiops truncatus*) in managed care have been observed to beach themselves on docks as early as 2 years 3 months of age, after observing their mothers perform the same behavior (Paulos et al., 2010), and belugas and killer whales in managed care spontaneously beach themselves as early as 3 months of age (Guarino et al., 2016; Hill, 2009; Hill & Ramirez, 2014).

Object play

Cetaceans play with or manipulate animate and inanimate, organic and inorganic objects in their environment, such as seaweed, nonprey animals, and man-made objects. Cetaceans can use their beak or rostrum to move objects, and their mouth to carry or toss objects. They often pass objects between their mouth, pectoral fins, and flukes, while sometimes carrying or balancing objects on their backs, sides, melon, or other body parts (Bender, 2012; Greene, Melillo-Sweeting, & Dudzinski, 2011; Hill & Ramirez, 2014; Kuczaj et al., 2006; Owen, Dunlop, & Donnelly, 2012). Bottlenose dolphins, dusky dolphins (*Lagenorhynchus obscurus*), rough-toothed dolphins (*Steno bredanensis*), Hector's dolphins (*Cephalorhynchus hectori*), Atlantic spotted dolphins (*Stenella frontalis*), and humpback whales (*Megaptera novaeangliae*) have all been observed engaging in similar behaviors with kelp, seaweed, and seagrass (as reviewed by Kuczaj & Eskelinen, 2014; Owen et al., 2012; Paulos et al., 2010). Free-ranging rough-toothed dolphins have been reported to play with plastic using behaviors similar to those observed during seaweed play (Kuczaj & Highfill, 2005; Kuczaj & Yeater, 2007). Similarly, bottlenose dolphins in managed care play with biological objects present in their habitats as well as with objects intentionally provided by humans or that unintentionally fell into the habitat (e.g., sunglasses, hats, papers). Many cetaceans in managed care display novel manipulations of objects within their habitat (e.g., young belugas attempt to balance on a large boomer ball while surfing it across the water, and young killer whales attempt to submerge large plastic barrels; H. Hill, personal observations) and repeat them until the behaviors are mastered, suggesting that play may augment the behavioral repertoire as a form of innovation.

It is important to note that not all object manipulation by cetaceans is play. Amazon River dolphins (*Inia geoffrensis*) carry floating vegetation, sticks, branches, and negatively buoyant hard clay as a socio-sexual display (Martin, da Silva, & Rothery, 2008). Unlike play, object carrying by Amazon River dolphins is overwhelmingly observed in adult males in the presence of adult females and other adult males. The carrying fluctuates with seasonal patterns of conception, despite the lack of variation in the objects' availability. Similarly, sponge carrying, exhibited by a small subsection of bottlenose dolphins (*Tursiops aduncus*; i.e., five females) in Shark Bay, Western Australia, is considered to be a form of tool use that aids foraging (Smolker, Richards, Connor, Mann, & Berggren, 1997). Despite these examples of functional object manipulation, the vast majority of object manipulations by cetaceans are considered playful.

Bubble play Although most individuals play with objects they find, capture, or are provided with, cetaceans in managed care, including belugas, bottlenose dolphins, and Amazon river dolphins, can create their own objects with which to play—bubbles (Bender, 2012; George & Noonan, 2016; Hill et al., 2011; Jones & Kuczaj, 2014; Kuczaj et al., 2006; McCowan, Marino, Vance, Walke, & Reiss, 2000). Cetaceans in their natural habitat use bubbles as part of their foraging tactics, but have also been observed to play with bubbles. A number of accounts exist that demonstrate that different species and different populations of the same species create and play with bubbles in a variety of ways. Most observations detail individuals using their blowholes and mouths to expel air and create bubbles of different sizes and shapes (e.g., bubble rings; McCowan et al., 2000). However, bottlenose dolphins have been observed to also use their flukes to create bubble rings by slapping the flukes on the surface of the water (McCowan et al., 2000; Pace, 2000), and belugas were observed creating underwater bubble helixes with their flukes (Jones & Kuczaj, 2014). Similarly, Gewalt (1989) observed Orinoco freshwater dolphins (*Inia geoffrensis*) in managed care utilizing a scrub brush as a tool to create bubble curtains as the brush was passed through the water. These examples illustrate the creativity in the creation and manipulation of different-shaped bubbles. Cetaceans can modify the trajectory of their bubbles by moving individual bubbles with their rostrums or directing water streams at them to move them about, or may simply observe them move through the water column. Cetaceans also produce additional bubbles that are then directed through larger rings or adjoined to the original ring (George & Noonan, 2016; Gewalt, 1989; Jones & Kuczaj, 2014; Kuczaj et al., 2006; McCowan et al., 2000; Pace, 2000). Part of bubble play is also to "creatively" or intentionally destroy the bubbles by biting them, swimming through them, or hitting them with various parts of the body (Gewalt, 1989; McCowan et al., 2000; Pace, 2000).

Social play

Although many play behaviors can be performed independently, if two or more individuals play together cooperatively, the play bout is then social. The cooperative nature of the interaction is what differentiates social play from various forms of solitary play (Parten, 1932; see Table 1). Solitary play can occur when one individual plays alone, but other solitary states include parallel play, during which multiple individuals play in a similar way or with similar objects within the vicinity of one another. Observational play occurs when one individual observes the play behavior of another. In contrast to social play, individuals do not engage in mutual or cooperative interactions (Bakeman & Brownlee, 1980; Goldman, 1981) during solitary, parallel, and observational forms of play.

Critical role of cooperation Because some aspect of cooperation is critical to the classification of social play, cooperation is also required during competitive play, such that the bout is continued until a "winner" is determined (Bauer & Smuts, 2007). Social play has been documented in individuals

residing in managed care or natural habitats of diverse cetacean species with few differences between these settings. Social play includes reciprocal chases, frequent body contact, and sexually oriented behaviors as well as shared object manipulation (e.g., passing seaweed between conspecifics or pushing a toy together).

One account of social play between bottlenose dolphins in Shark Bay, Australia, involved herding play, during which individuals performed role reversals within a play bout, such that one acted as a pursing dolphin and then as the dolphin being herded (as described in Paulos et al., 2010). Role reversals between dominant and submissive individuals, as well as self-handicapping or inhibiting oneself by swimming at a slower speed, encourages disadvantaged players to participate in play with more experienced partners (Bender, 2012; Kuczaj & Eskelinen, 2014). A similar social-play interaction has been observed with belugas in managed care playing "king of the hill" (described in Hill & Ramirez, 2014). The observations of this "game" involved two to three belugas participating with each of them taking turns on an underwater shelf, although additional examination will be needed to determine whether there are consistent winners or losers.

It can be difficult to delineate between social play, sexual behavior, and aggression in cetaceans. Social interactions can suddenly transition from one type of interaction to another and the presence of aggressive or sexual *behaviors* does not preclude the possibility that the interaction is playful. All definitions of play indicate that some elements of a species' behavioral repertoire can be incorporated into play bouts (Burghardt, 2005). One example of this ambiguity involves the nature of mouth behaviors displayed by bottlenose dolphins and belugas. Different variations of mouth behaviors such as wide open mouth displays of aggression, gentle mouthing on a conspecific typical of socio-sexual interactions, and more intense aggressive-style biting are used in play interactions (Kuczaj & Frick, 2015). More intense biting that produces rake marks (i.e., surface abrasion caused by teeth) is often seen in aggressive encounters, however more research is necessary on this topic as depth and location of rake marks may discriminate between types of social interaction (K. Dudzinski, personal communication, July 4, 2017). Although human observers may have difficulty discriminating the context of a specific mouthing event, cetaceans seem to discriminate these contexts fairly quickly.

A unique form of mouth-to-mouth social interactions, preliminarily considered a form of play, have been documented between beluga calves (Connor & Peterson, 1994; Dietrich, Garza, Hill, & Aibel, 2013; Krasnova, Chernetsky, Zheludkova, & Bel'kovich, 2014). This form of mouth-to-mouth interaction is highly cooperative. First, calves must mutually meet head-to-head. Then the calves must coordinate their positions to lock mouths; sometimes one rotates while the other remains stationary and other times they both rotate on their sides. Finally, the calves must keep enough pressure to remain attached without hurting the other calf (Dietrich et al., 2013). Sustained mouth-to-mouth contact of this form has not been observed to occur in other cetaceans or between adult female belugas.

Partner selectivity Constrained by availability, cetaceans may select partners with which they prefer to play. Over the first two months of life social play primarily occurs between mother and offspring (Guarino et al., 2016; Hill, 2009; Hill, Campbell, Dalton, & Osborn, 2013; Mann & Smuts, 1999). Partner selectivity for same age peers begins to develop as the frequency of play increases with young calves typically associating with one individual closest in age to themselves (Hill & Ramirez, 2014; Jones & Kuczaj, 2014; Kuczaj et al., 2006; Mackey, Makecha, & Kuczaj, 2014). As calves age, older and more competent peers are selected for play interactions instead of same-age peers, possibly as a way to test their abilities (Baldwin & Baldwin, 1978; Kuczaj et al., 2006; Mackey et al., 2014).

Some cetaceans may also prefer same-sex partners when choices are available for social play (Connor, Wells, Mann, & Read, 2000; Glabicky, DuBrava, & Noonan, 2010; Hill, Dietrich, et al., 2015; Mann & Smuts, 1999). For example, Hill, Dietrich, et al. (2015) found that when beluga social groupings in managed care were mixed between different ages and sexes, the older male belugas preferred to engage in social interactions with each other that were best categorized as socio-sexual play: The adult and subadult males displayed reciprocal role reversals such that one was the dominant initiator and the other was the submissive receiver until the roles were reversed mutually. This pattern of behavior was observed with a different group of belugas in managed care (Glabicky et al., 2010) as well as in dolphins in managed care and their natural habitat (reviewed by Connor et al., 2000). Partner selectivity has been measured primarily for whales and dolphins in managed care and provisioned dolphins in Shark Bay, and is thus relatively unknown in their wild counterparts.

Interspecies social play Sometimes cetaceans choose to play with animals of different species. In some instances, these events are classified as social play and other times they are considered examples of object play. Although prey are typically manipulated functionally during feeding, cetaceans have been observed tossing, hitting, and catching and releasing their prey prior to consumption (Paulos et al., 2010). At Monkey Mia in Australia, wild juvenile bottlenose dolphins were observed to chase prey but did not capture or consume it, categorizing this behavior as play (Mann & Smuts, 1999). Similarly, spotted dolphins, bottlenose dolphins (Greene et al., 2011), and Australian humpback dolphins (*Sousa sahulensis*; Barber, 2016) have been observed carrying nonprey items, such as puffer fish, jellyfish, or other species that may inhabit their environment (e.g., starfish, turtles, and even birds), which has been interpreted as play behavior.

Although these interactions with prey and nonprey items may be categorized as object play, cetaceans may also play with other marine mammals, which can be categorized as either social play or both object and social play. One report describes interactions between a bottlenose dolphins and a humpback whale in which the whale lifted a dolphin out of the water repeatedly for no clear reason (Deakos, Branstetter, Maxxuca, Fertl, & Mobley, 2010). Under these circumstances, whereas the whale may have been engaging in object play, the dolphin seemed to be engaging in social play, as this behavior required the cooperation of both animals (Deakos et al., 2010). Accounts of interspecies social play include bottlenose dolphins herding fur seals (*Arctocephalus pusillus*), as well as short-finned pilot whales (*Globicephala macrorhynchus*) performing a similar herding behavior around sperm whales (*Physeter macrocephalus*; summarized in Paulos et al., 2010). Belugas housed in adjacent pools with visual access to Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) have been observed to synchronize their swims with each other, displaying fast swims (indicated by white water and wave action), leaps, sudden turns, and "face offs" in which each animal repeatedly "charges" the other but without accompanying aggressive actions (H. Hill, personal observation). Similarly, wild bottlenose dolphins have been observed to interact socially with spotted dolphins (Herzing & Johnson, 1997; Herzing, Moewe, & Brunnick, 2003). Bottlenose dolphins in managed care will even "play" with humans whether it is tossing a ball back and forth (Highfill, Yeater, & Kuczaj, 2016) or engaging in a game of "hide-and-seek."

Not all interspecific play interactions end peacefully. In Scotland, bottlenose dolphins were documented chasing, fluke hitting, and throwing harbor porpoises, resulting in the death of the harbor porpoises (*Phocoena phocoena*; as cited by Paulos et al., 2010). Similarly, whereas wild bottlenose dolphins at Monkey Mia in Australia have been observed playing peaceful games passing seaweed back and forth, dolphins may also harass humans (Mann & Smuts, 1999) and even pull individuals standing nearby into their pools (Paulos et al., 2010). Killer whales in their natural habitat and in managed care catch birds by first baiting them with pieces of fish, then lurking below the water's surface, and finally surging forward to capture the bird (Paulos et al., 2010). Killer whales will also play with their mammalian prey, often tossing it repeatedly in the air and hitting it with their flukes, before releasing it (Baird, 2000).

Play varies across species and environments

Although the different suborders under Cetacea—Odontocetes and Mysticetes—display many of the same behaviors during play (e.g., riding bow waves of boats, aerial maneuvers, and erratic swims), some variation occurs for types of play and frequency of play across different populations. On the basis of a limited number of studies in which play behaviors were systematically examined in natural habitats, play appears to be regulated by multiple factors, such as food availability, object accessibility, and environmental protection (rough-toothed dolphins: Kuczaj & Yeater, 2007; bottlenose dolphins: Greene et al., 2011; Weaver & Kuczaj, 2016; Australian humpback dolphins: Barber, 2016).

Increased food availability and safety from predators encourages play behaviors (Burghardt, 2005). Coastal bottlenose dolphins, for example, exhibit more play behaviors than spinner dolphins (*Stenella longirostris*) or common dolphins (*Delphinus* sp.; Janik, 2015). Coastal bottlenose dolphins spend more time in the safer near-shore waters where exposure to predation is limited, and spend less of their time traveling, compared with spinner or common dolphins. Predator–prey status and physical size may influence the expression of play behaviors by a population. Cetaceans that have predator status (e.g., killer whales and bottlenose dolphins) or are physically large (e.g., sperm whales, baleen whales) may have more opportunities to play given the absence of predators.

Overall, 37 different types of play have been documented for dolphins in managed care (Kuczaj et al., 2006) and the types of objects appear to differ between individuals in their natural habitat versus managed care (Bender, 2012; Gewalt, 1989; Greene et al., 2011; Kuczaj & Eskelinen, 2014; Kuczaj et al., 2006). These patterns should be interpreted cautiously as variation in observed play is greatly influenced by the researcher's ability to view animals clearly. Patterns of play frequency vary with visibility: (1) cetaceans in managed care are the most readily observable and play is observed most often, and (2) play is observed more often by near-shore animals than the less visible offshore cetaceans. Purely descriptive explanations place the sole burden of empirical proof on the observation of behavior, limiting generalization between species and contexts.

Theoretical approaches to play: Organizing the current knowledge

Like other animals, the ultimate puzzle of cetacean play is its function. Although defining, identifying, and cataloging play across species of Cetacea is no trivial task, searching for the function of an activity defined by its *lack* of immediate functionality can seem almost paradoxical. Thus far, many of the functions examined in other animals have consisted of the indirect and long-term benefits of play for an individual player or the population. Psychological theories, such as Piaget's cognitive development theory and Parten's social-play states, have established sequences for typical human development, marked by significant milestones. These perspectives offer useful comparisons for understanding animal play, especially in long-lived, socially complex species with extended periods

of development. The established theories offer standards and methodologies that may be applied to numerous species, and which can also be used to assess ultimate questions of evolutionary history and function, as well as proximate questions of ontogeny and genetic mechanisms—questions that continue to be difficult to assess for the concept of play. The establishment of species-typical standards for healthy development across the lifespan can assist in managing the welfare of animals in managed care. For these animals' wild counterparts, knowledge of developmental progression can be used to inform regulations and protect populations from negative exposure during particularly sensitive periods.

Developmental approaches

Groos's practice theory of play

A revolutionary voice for his time, Groos (1898, 1901) proposed a Darwinian-inspired explanation for play. The "play as practice" theory put forward by Groos viewed the function of play as developing instinctual capacities to maturity and learning noninstinctual skills (Groos, 1901). He proposed that intellectually complex animals necessitated longer periods of immaturity, dependent on their parents, to develop through play. Groos went so far as to write: "Perhaps the very existence of youth is due in part to the necessity for play; the animal does not play because he is young, he has a period of youth because he must play (Groos, 1898, p. 76). Groos's practice theory of play begins on the premise that immaturity at birth and a prolonged period of maturation are advantageous (Table 2).

Cetacean calves are born precocial with the ability to swim immediately at birth, which is followed by a strong following response similar to ungulates. Yet cetaceans, like primates and unlike most precocial species, are born at a premature stage of development and have long periods of infancy. Cetacean calves are limited in their ability to direct their swimming, to maintain buoyancy, and to propel themselves forward for long periods of time (Noren, Biedenbach, & Edwards, 2006; reviewed by Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008). For the first month, calves swim almost continuously with their mother or an alloparent (babysitter) and are entirely dependent for milk and protection prior to weaning (Asper, Young, & Walsh, 1988; Cockcroft & Ross, 1990; McBride & Kritzler, 1951; Thomas & Taber, 1984). Postweaning, offspring continue to learn from their mothers, which allows the calves time to learn complex behaviors (Bender, Herzing, & Bjorklund, 2009; Mann & Smuts, 1999) and is consistent with Groos's practice theory (Table 2).

Play as practice is commonly referenced as an explanation for the locomotor play of infant cetaceans (reviewed by Kuczaj & Eskelinen, 2014). Locomotor play begins around the first and second months of life in many of the observed species of Odontocetes (Table 2). During this time, cetacean calves are developing their swimming fitness and skill. Locomotor play-type behaviors of calves have been noted among Mysticetes but are not as well documented for Odontocetes (e.g., humpback whales: Clapham, 2000; southern right whales: Thomas & Taber, 1984). As is summarized in Table 2, southern right whales, a species of baleen whale, show motor play development that supports Groos's notion that play is important for practicing future behavior (Thomas & Taber, 1984). As early as one month, calves engage in periods of independent, mother-centered locomotor play, which increases gradually between the second and fourth months of life. At four months, the annual migration abruptly restricts the levels of play until the calves are brought together in social groupings of similar-aged cohorts and play reemerges (Thomas & Taber, 1984). For bottlenose dolphins in Shark Bay, the earliest play observed takes on similar forms of locomotor "practice" behavior, although more research is needed to document the development process (Mann & Smuts, 1999).

The same trend was found in a 10-year study of the behavioral development of belugas in managed care. Beluga calves "practiced" (e.g., repeated behaviors that were incomplete and awkward) spy hops, back breaches, and floating at the surface during the first 2–3 months of life in the presence of their mothers, apparently working to acquire control of their bodies. Following mastery of these behaviors, spin swims, bows, and other types of body slaps and aerials began to emerge more frequently (H. Hill, personal observation).

Table 2 Summary of Groos's theory of play as practice and relevant examples

Groos (1898, 1901)	Humans	Odontocetes	Mysticetes
Instinctual capacities are developed during a period of immaturity	Reflexive motor behavior is refined through period of dependence (e.g., manipulating objects, rolling, sitting up, walking, running, jumping)	Develop swimming, fitness, and buoyancy control through locomotor play (1–3 mo)	Mother centered locomotor play (1 mo) Time spent playing increases (2–4 mo)
Noninstinctual capacities are developed after reaching maturity	Intentional control over actions performed once as play, but now functional (e.g., jumping to retrieve object, running to get away)	Develop motor control of air release through object play with bubbles (2–4 mo). Believed to provide practice for behaviors with a functional significance as adults	Play restricted for migration (4 mo) Play reemerges when social group includes same-age cohorts

Developmental stage theories of play

First 4 months' and older play in terms of Piaget's sensorimotor stage Piagetian theory of cognitive development influenced a number of aspects of developmental psychology, including understanding play by human children (Brooker, Blaise, & Edwards, 2014). Development, as discussed by Piaget, progressed through a series of stages (Table 3). By extension, he expected the primary form of play at each age to correspond with the cognitive-developmental stage. The first stage of development for Piaget is the "sensorimotor." Early substages of the sensorimotor stage center around motor development, then progressively become more focused on advanced forms of cognition. The later stages of development (i.e., preoperational, concrete, and formal) theorized by Piaget are difficult to assess comparably in nonhuman species, since the stages center around the understanding of symbols, classification, abstract thinking, logical reasoning, and metacognition (Table 3). However, Piaget's first stage of development provides a useful framework for the developmental stages of cetaceans and for the form and function of play expected at each substage.

Beginning at birth for human children, and lasting until 2 years of age, these children as described by Piaget's sensorimotor stage are preoccupied with their own body movements, sensory experiences, and how those actions can influence the world around them. Babies' actions are initially guided by reflexes until they develop schemata through trial and error. Play is focused around the concept of being a "little scientist." Through play, children learn the functional use of an object by increasingly complex and novel misuse (Table 3). In dolphins, belugas, and other large whales, an examination of anecdotal reports of locomotor play suggests that neonates progress from early nonfunctional movements, such as out-of-control body slaps, leaps, and floppy flukes (e.g., Clapham, 2000; Cockcroft & Ross, 1990; Hill, 2009; Mann & Smuts, 1999), to functional social displays used in nonfunctional contexts (Table 3).

Dusky and bottlenose dolphins have several distinct leaps that appear in specific functional contexts for adults. Initial leaps for dolphin calves are unsophisticated "noisy leaps," with the dolphin "flopping" back into the water. Clean leaps are developed after noisy leaping (Chechina, 2009; Deutsch, Pearson, & Würsig, 2014). More sophisticated "coordinated leaps" are first seen in early-yearling dusky dolphins with late-yearlings showing all four major kinds of leaps: noisy, clean, acrobatic, and group-coordinated (Deutsch et al., 2014). Dusky dolphin calves do not modulate their type of leap by behavioral state in the same way as adults, indicating that calves learned the behavioral patterns prior to learning the functional context. The calves appear to develop the motor patterns of leaping through solo play, then integrate leaps into social contexts, possibly through social play with peers (Deutsch et al., 2014).

Young wild dolphin calves chase fish erratically while also manipulating various organic and inorganic objects within their environment, such as feces, self-produced bubbles, seaweed, or seagrass. Playing with fish develops into "snack" foraging near 3 months of age, in which the calves swim belly up to chase, catch, and release prey fish (Mann & Smuts, 1999). During "snack" foraging, dolphin calves are displaying functional feeding behaviors in a nonfunctional, playful, context as would be expected in Piaget's sensorimotor period.

Similarly, between 2 and 4 months, beluga calves start to emit bubbles of various sizes with differing levels of control, as they "practice" releasing air through their blowhole in different ways. This rehearsal may be another method to acquire motor control over a behavior that has functional significance as an adult. Adult belugas produce bubble bursts as displays for different contexts including surprising, threatening, and protective situations (Hill et al., 2011).

The progression of play through Piaget's sensorimotor stage can be most readily observed in cetaceans in managed care. Play behaviors with objects provided by humans may reflect functional significance similar to their wild counterparts. Animals in managed care will combine object manipulation with behaviors already present in their behavioral repertoire, like tossing a buoy or a ball while swimming, carrying a pot on one's head while swimming, holding a small plastic bucket under one pectoral fin, carrying a flexible strap draped across a pectoral fin, head, or body, or tossing a pair of sunglasses (that had fallen into the pool) into the air and catching them with the mouth (Hill & Ramirez, 2014; Kuczaj et al., 2006). Tossing and carrying objects are seen as functional parts of the adult behavioral repertoire (i.e., calf carrying behavior by mothers, Kilborn, 1994).

As calves mature, they begin to perform different and novel behaviors with novel and familiar objects alike, creating more complex interactions with objects (see Secondary and Tertiary Circular Reactions in Table 3). Beluga calves have been observed attempting to trap a ball underwater with different body parts, including by their head, full body, flukes, and pectoral fins. One dolphin calf was documented dropping a water-filled ball from the surface and attempted to catch it with different body parts before the ball hit the bottom of the pool. By manipulating novel objects in familiar or innovative ways, these young animals are illustrating Piaget's concept of a "little scientist" as they move through the sensorimotor stage while also adding a component of unpredictability to their play, making it more stimulating or cognitively challenging (Bender, 2012; Kuczaj & Eskelinen, 2014).

This comparison of the sensorimotor stage of development (the first 2 years of human life) to early cetacean development (approximately the first 12 months of life) is not meant to say that dolphin development is "comparable" to human development at that time. Rather, the comparison emphasizes the utility of developmental stage theories for studying cetacean development. Using a theoretical model from psychology

Table 3 Sensorimotor stage of Piaget's (1951) cognitive developmental theory: Summary and examples

	Description	Humans	Cetaceans
Sensorimotor Stage		Birth–2 yr	Yearlings
Reflexive Behavior	Behaviors are primarily reactions to external stimuli	Sucking anything placed in mouth, basic reflexive behavior (Birth–1 mo)	Nonfunctional locomotor displays: out-of-control body slaps, partial leaps, and floppy flukes (Birth–1 mo)
Primary Circular Reactions	Practice or functional play through locomotor play	Sucking thumbs, kicking legs, moving arms (2–5 mo)	More controlled locomotor displays: body slaps, tail slaps, breaches (2–4 mo)
Secondary Circular Reactions	Nonconventional and nonfunctional object play	Shaking rattle, banging spoon, hat on and off head (5–10 mo)	Object manipulation is combined with functional behaviors in behavioral repertoire: snack foraging at 3 mo; tail slaps, repetitive object play (3–12 mo)
Tertiary Circular Reactions	Functional actions toward conventional objects	Throw spoon down to be picked up repeatedly, Peek-a-boo (10–18 mo)	Socially functional displays such as clean and coordinated leaps under nonfunctional contexts (4–12 mo)
Preoperational, Concrete, & Formal Operational Stages		2–12+ yr	Unknown–Adulthood
	Centers around the understanding of symbols, classification, abstract thinking, logical reasoning, and metacognition	Object permanence, language, concrete operations, transformations to appearance, deductive reasoning, theory-of-mind tasks	Developmental milestones tested in cetaceans include the discrimination between familiar and unfamiliar people, object permanence, and attribution of theory of mind (adults)

provides a foundation for comparative studies of developmental function that can be adapted to animals from all environments and phylogenies.

The onset and maturation of cetacean social play viewed through Parten's social-play hierarchy (4–12 months) Parten's (1932) social theory of play categorizes play by the level of social participation in preschool children (2–5 years of age). Children are thought to progress through six sequential levels: unoccupied behavior, solitary play, onlooker behavior, parallel play, associative play, and cooperative play. Cooperative play is regarded as the most mature level of peer interaction (Table 4). Unlike Piaget's theory of cognitive development, Parten's play stages can be visually observed without intervention in natural settings. In addition, as a set of purely behavioral measures, Parten's hierarchy is readily applicable to cetacean play.

The first of Parten's classifications, unoccupied behavior, involves passive observation of the environment and limited locomotor play. As Parten writes, "When there is nothing taking place, he plays with his own body, gets on and off chairs, just stands around, follows the teacher, or sits in one spot glancing around the room" (1932, p. 249). The second classification defines solitary independent play as playing with toys without making an effort to be close to or engage with other children. "He pursues his own activity without reference to what others are doing" (p. 250). The next step in Parten's hierarchy is onlooker behavior, in which the child actively watches or interacts with a play group but does not join in the play. The fourth pre-social-play classification is parallel play, in which a child plays alongside but not with other children. Play characterized by true social interaction begins after these four stages (Table 4).

The initial 3–4 months of cetacean play are prior to the onset of peer social-play interactions (Table 4). Play seen prior to around 3–4 months of age is almost exclusively performed alone. Similar to the onlooker behavior described by Parten (1932), calves spend most of their time swimming with their mothers, typically in a position that allows them to view activities going on around them and those in which their mothers are actively involved (e.g., Sargeant & Mann, 2009). Calves are often reported to orient toward the activities of others while swimming near the action.

In accordance with the progressive stages of Parten's (1932) hierarchy, cetacean play progresses from solitary play, through an intermediary play that matches some definitions of onlooker or parallel play, to social play. At around 3–4 months of age, dolphin calves engage in locomotor or object play within the proximity of other calves. This parallel-style play is still solitary play, since each calf has its own goal, and there is very little coordination between the other calves in close proximity. Mann and Smuts (1999) reported that dolphin calves dropped, but did not pick up and pass, sea grass to one another early on, perhaps representing a form of parallel play (Table 4). The onset of social play is classified by two successive levels: associative play and cooperative supplementary play (Table 4). *Associative* play is the first level of truly social play in which objects may be shared but

Table 4 Parten's (1932) developmental stages of social play: Summary and relevant examples

	Description	Humans	Cetaceans
		4 mo–5 yr	Birth–Yearling
Unoccupied Behavior	Passive observation of the environment and limited locomotor play	Watch activities within the environment, rolling, climbing, moving limbs	Calf swims with mother throughout the environment with limited solo swims or motor manipulations
Solitary	Independent play such as playing with toys without making an effort to be close to or engage with other children	Play with toys alone without regard for peers	Play is almost exclusively independent, mainly locomotor play and maybe object play (prior to 3–4 mo)
Onlooker	The child actively watches or interacts with a play group but does not join in the play	A child is playing with cars or blocks near another child who is watching but not engaging	Learning to forage or socialize as swim with mother in specific positions to allow them to view activities of the mother (3–5 mo)
Parallel	The child plays alongside but not *with* other children	Both children play with cars while sitting next to one another but not interacting with each other	Locomotor or object play by one calf within the proximity of other calves (5–12 mo)
		12 mo–5 yr	3 mo+
Associative	Materials are shared between the children but the play lacks any level of order with members of the group	Blocks are shared between two children but the children are not working together to build a wall, rather may be working to build two separate walls of their own	Tactile interactions between calves and their mothers or pair swims and chases with other young conspecifics
Cooperative	Children work together to achieve play goals and can be organized by a leader to take on different roles	Children use blocks to build a home, working together on a single goal	Complex forms of social play requiring coordination, reciprocation, turn-taking: (1) reciprocal "face offs" of "aggressive" behaviors, (2) "king of the hill or shelf," (3) reciprocal socio-sexual interactions, and (4) manipulating large objects

coordination toward a common goal is lacking. *Cooperative* play is the pinnacle of social play, in which all aspects of play are needed: motor skills, cognitive skills, turn taking, cooperation, and a common goal.

In accordance with Parten's (1932) hierarchy, truly social play in cetaceans begins simply and increases in complexity with age. Cooperation in cetaceans during social play is quantified as turn taking, coordination, or reciprocal behaviors (Table 4; Félix, 2015; Kuczaj, Winship, & Eskelinen, 2015; Paulos et al., 2010). Simple social play in dolphins and beluga calves begins with calves initiating tactile interactions with their mothers. From these social-play interactions, calves will then engage in pair swims and chases with other young conspecifics, if they are present (Table 4). More complex forms of social play appear as games in which multiple turns and types of play are present (Table 4).

Developmental milestones and sensitive periods

Stages of play correspond with developmental progression and indicate the function of play in physical, cognitive, and social development. Play is both an observable method of determining species-typical developmental changes occurring at specific ages and an indicator of atypical development of an individual. The developmental role of play can be seen most overtly by examining two related domains: developmental milestones and critical/sensitive periods.

Play during development is proposed to facilitate the achievement of developmental milestones. Like humans who achieve physical developmental milestones at specified ages during the first year of life (e.g., rolling, sitting up, crawling, walking), cetacean calves also progress through a sequential physical development with specific milestones. For example, neonatal breathing (i.e., shooting up out of the water like a rocketship) progresses to smoother breathing patterns (Noren et al., 2006) after maturation and practice. The ability of young calves to float and dive down from the surface is limited while their fat content is high and they lack buoyancy control (Noren et al., 2006, reviewed by Lyamin et al., 2008). Calves between 1 and 4 months of age have been observed to

"practice floating" at the surface, from where they gradually begin to submerge themselves, but then pop up like a block of ice after losing control of their float (H. Hill, personal observation). Mastery of swimming within the water column and of general body movements (fast swims, rapid turns, aerials, beaching) is part of the locomotor play repertoire and appears to be organized by developmental milestones, since most calves master these skills around the same age, possibly indicating healthy development. These locomotor play activities appear to parallel human developmental milestones (see Table 3 for a summary of Piaget's age-based milestones).

In humans, and likely in cetaceans, the sensorimotor period integrates physical with cognitive development. Human children achieve several critical cognitive milestones by the end of the sensorimotor period: the abilities to distinguish themselves as an individual from another human, to discriminate between familiar and strange people, and to recognize that people and objects continue to exist even if they disappear from sight. Many of these skills come through repeated experiences, including such games as peek-a-boo or "let's throw the rattle and have that other person pick it up." Likewise, through games human infants begin to learn that their actions can affect other people, which corresponds to a progression in play states, from solitary play and observer behaviors to increasingly complex social play (Parten, 1932). Increased social interactions, especially during play bouts, allow children to practice role reversals, to take turns, to take risks, and to make reparations. Preschoolers learn about taking the perspectives of others, and by the time they are 5 years old have achieved full theory of mind, which allows them to make attributions about others' mental states and knowledge (e.g., engaging in deception or empathy; for a review of theory of mind and developmental milestones, see Hughes & Leekam, 2004).

Cetaceans (e.g., dolphins, belugas, and lags) can provide useful comparative evidence for such theories of the development of object permanence (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010; Johnson, Sullivan, Buck, Trexel, & Scarpuzzi, 2015), cognitive milestones (Hill et al., 2016; Thieltges, Lemasson, Kuczaj, Boye, & Blois-Heulin, 2011), and theory of mind (Kuczaj, Tranel, Trone, & Hill, 2001; Pack & Herman, 2004; Tschudin, 2001). Testing developmental milestone achievement as cetacean calves age could bridge the current gap between observable behaviors and social–cognitive development. Studies conducted with Odontocete populations in managed care could determine the extent to which easily observable behaviors, such as type and frequency of play, are indicative of developmental milestone achievement. This research would paint a cohesive picture of calf developmental stages and, most critically, of the behaviors that indicate healthy development. Identifying observable indicators of social and cognitive development would have wide-ranging applications for cetaceans in both managed and wild contexts. On the basis of developmental stage theories, we would predict that the onset of advanced cognitive abilities will be influenced by the play behaviors characteristic of earlier developmental stages.

Animal-specific hierarchies of play

Researchers of animal play have proposed different graded or hierarchical classification systems that are similar to developmental stage theories but do not have the same assumptions as true stage theories (i.e., that invariant, fixed sequences are exhibited by species at certain points in time with qualitative differences). One classification scheme with aspects of a stage theory is Fagen's (1995) approach, in which play progresses to more complex forms, from single, noninteractive actions that are repeated to play that involves social interactions of different forms (Table 5). These later forms include "games" with others and more complex forms of solitary locomotor or object play. As play becomes more complex, animals begin to include other conspecifics, objects, and environmental components, with the most cognitively complex form of play being social play that involves attribution of knowledge on the part of one of the participants (e.g., mother tutors/assists offspring during a play bout). Fagen did not identify specific cognitive abilities that would be needed at each level of the classification scheme, and as Burghardt (2005) indicated in his review, some of the examples identified by Fagen appeared to be arbitrary rather than following a logical argument based on cognitive abilities. Mitchell's (1990) approach may help rectify this issue, by introducing a role for intentionality in the hierarchical classification scheme (Table 5).

Although Mitchell (1990) and Fagen (1995) did not intend to classify animal play from a developmental perspective, the behaviors identified at each level of their hierarchies map onto Piaget's and Parten's theories of development. Both animal-based perspectives proposed that the first levels of play include basic locomotor actions (e.g., early part of Piaget's sensorimotor period). By the second level in both animal perspectives, play becomes progressively more complex, similar to the later substages of Piaget's sensorimotor period (cf. Tables 3 and 5). The ultimate form of play, *pretense play*, is considered in Fagen's last level and Mitchell's last two levels of animal play. These higher-level play activities depend on the player's ability to mentally represent real and imagined events and then act out those representations independently and in coordination with another individual (Table 5). In humans these activities are called *cooperative imaginative play*. Most human children cannot achieve this level of sophistication until their preschool years, even though they develop simple forms of symbolic thinking and engaging in complex social play by the end of their second year (Parten, 1932; Piaget, 1951). Coordinating games of pretend is a skill that develops between 3 and 5 years of age (Lillard, 2015). Although it is *possible* that animal play involves pretense, it

Table 5 Hierarchical animal play theories: Summary and relevant examples

Fagen (1995)	Mitchell (1990)	Cetaceans
Level 1	*Level 1*	*Level 1*
Noninteractive solitary forms of locomotor and object play	Basic locomotor actions	Solitary locomotor and object activities: body slaps, floating, ventral swim, spiral swim; manipulate toys provided
Level 2	*Level 2*	*Level 2*
More complex play that incorporates other conspecifics, objects, and environmental components	Progressively more complex play	Incorporate multiple objects, other animals, different play types into play
Level 3	*Level 3 & 4*	*Level 3+*
Attribution of knowledge of one participant (e.g., mother tutors/assists off-spring during a play bout) Pretense may occur	Depends on the player's ability to mentally represent real and imagined events, then act out those representations independently and in coordination with another individual (cooperative imaginative play) Coordinating games of pretend (3–5 yrs)	Handful of anecdotes that may suggest some pretense, but not consistent. mothers may assist offspring during play bout

is difficult to assess pretense in animals, since mental states can only be inferred on the basis of actions. Animals cannot be asked what they are thinking about when they display an unexpected behavior, such as when a dolphin calf squirted milk in the shape of a cigarette smoke puff after observing a human create one (Tayler & Saayman, 1973).

Summary of theoretical perspectives on cetacean play

We have reviewed cetacean play utilizing several different developmental theories and perspectives (Table 6). Most models of play development converge at the onset of play, anticipating that an animal's earliest play will take on the simplest form: locomotor solitary play (Fagen, 1995; Mitchell, 1990; Piaget, 1951; Parten, 1932). Early locomotor play is often explained as "practice" for developing bodily control, sensory systems, and environmental understanding (Groos, 1898). All theories of play anticipate an increase in complexity as an animal develops. The theories diverge, however, on the underlying mechanisms of play advancement. Fagen and Piaget described advanced play as involving pretense and mental schemas—constructs that are difficult to assess in cetaceans.

Parten's hierarchy of social play provides the most utility for quantifying the more complex social play observed in cetaceans, from a developmental perspective. Many, although not all, species of cetaceans are highly social, with complex social structures. Categorizing the development of play in terms of increasing social complexity is consistent with the ecological pressures on cetaceans. Future research should compare play between more and less socially complex cetacean populations in order to determine the fit of Parten's hierarchy across cetacean social structures and to further knowledge of the relationship between the development of play in calves and of adult sociality.

Approaching cetacean play using developmental theories allows for organizing the findings on play according to function, rather than a play behavior's appearance, which can facilitate comparisons between species in terms of sequence, function, and age of onset. Moreover, connecting observations of play to sensitive periods and developmental milestones would provide a useful blueprint for the management, welfare, and conservation of cetaceans. This knowledge, integrated with observations of social development, future survival, and reproductive behaviors, may refine our current understanding of the developmental stages of some cetaceans, which are currently defined by age, morphology (i.e., size, coloration), and sexual maturity.

Cetacean play across the lifespan and society

Play is not just for young cetaceans. Calf, juvenile, and adult cetaceans play in mixed-age groups, same-age groups, and independently. Purely developmental theories of play are insufficient to explain the potentially multifaceted roles of play across the cetacean lifespan and within cetacean societies.

Adult play

Play is considered a part of adult behavioral repertoires for all species of Cetacea, although it has been studied most often with belugas and a variety of dolphins in managed care and with certain populations in their natural habitat (e.g., Bender, 2012; Greene et al., 2011; Hill & Ramirez, 2014; Jones & Kuczaj, 2014; Kuczaj et al., 2006; Mackey et al., 2014). Play in adulthood differs in its forms and is thought to have distinct functions and motivations from developmental play. Whereas play in young animals is proposed to have potential long-term benefits, adult play may be more immediately rewarding. General theories of adult play suggest that it may be an artifact of surplus energy (Spencer, 1873) or a result of neoteny, in which immaturity is preserved into adulthood (Cairns 1976; Mason, 1968). From the neoteny perspective, adult play has been suggested to help retain flexibility and skill adaptation as an animal ages (Bekoff, 1972).

Table 6 A summary of play behavior in cetacean calves using different developmental and play theories

Cetacean Age	Piaget (1951)	Parten (1932)	Fagan (1995) & Mitchell (1990)
0–4 mo.	**Sensorimotor:** ***Primary Circular reactions*** Nonfunctional locomotor displays (Clapham, 2000; Cockcroft & Ross, 1990; Hill, 2009; Mann & Smuts, 1999; Thomas & Taber, 1984); Nonfunctional object manipulation (Hill et al., 2011)	**Solitary:** Independent play: locomotor, object **Onlooker:** During calf swims with their mothers (e.g., Sargeant & Mann, 2009) **Parallel:** Engage in locomotor or object play within the proximity of other calves, with no coordination (e.g., Mann & Smuts, 1999)	**Locomotor:** Single, repeated, noninteractive locomotor actions
4–12 mo.	**Sensorimotor:** ***Secondary & Tertiary Circular Reactions*** Functional displays: Leaps (Chechina, 2009; Deutsch et al., 2014); Object manipulation with known and innovated behaviors using familiar or novel objects (Hill & Ramirez, 2014; Kuczaj et al., 2006; Mann & Smuts, 1999)	**Associative:** Calf-initiated tactile interactions with mothers; pair swims, chases with other young conspecifics (Hill, 2009; Hill et al., 2013; Hill & Ramirez, 2014; Mann & Smuts, 1999) **Cooperative Supplementary:** Turn taking, coordination, or reciprocal behaviors (Félix, 2015; Kuczaj et al., 2015; Paulos et al., 2010) **Complex Social Play:** Reciprocal aggressive behaviors, surfing one another off of shallow raised areas, reciprocal socio-sexual interactions, and pushing and manipulating objects too large for a single calf (e.g., Hill, Guarino, et al., 2015; Hill & Ramirez, 2014)	**Complex Play:** Object play, social games
12+ mo.	**Preoperational, Concrete, and Formal Operations:** Discrimination between familiar and unfamiliar people (Hill et al., 2016; Thieltges et al., 2011); object permanence (Jaakkola et al., 2010; Johnson et al., 2015); attributions, theory of mind (Kuczaj et al., 2001; Pack & Herman, 2004; Tschudin, 2001)		**Pretense:** Anecdotal evidence only (e.g., Tayler & Saayman, 1973)

Table descriptions are derived from Piaget (1951), Parten (1932), Fagen (1995), and Mitchell (1990). Please see the original sources for additional explanation if you are interested. Efforts to correlate the timing of different stages of cetacean play with the human-based stages of development and theories highlighted are subject to revision with additional research and may differ across cetacean species.

Unfortunately, neither theory has gained much support through the various research efforts on play. Other likely explanations of play by individual adult animals include responses to the increased arousal of conspecifics or to individual boredom (reviewed in Burghardt, 2005). As in many terrestrial animals, play in adult cetaceans remains relatively underexamined.

Adult cetaceans will play socially with other adults, juveniles, and infants, but these opportunities are determined in part by social grouping and access to potential partners. For example, killer whales and sperm whales (*Physeter microcephalus*) form family units that stay together across the lifespan, whereas smaller delphinids and whales form fission–fusion societies that constantly reconfigure (reviewed by Connor, 2000). Some of these societies fission seasonally, with juveniles and/or adult males leaving the mother-infant groups. Others, such as most Mysticetes, tend to display primarily solitary lifestyles (blue whale *Balaenoptera musculus*, grey whales *Eschrichtius robustus*: Connor, 2000). Research with animals in managed care, in which social groups may be modified from naturally occurring groupings in the wild, can delineate the extent to which playmate selectivity is determined by availability.

Given these vastly different social structures, play may have different functions depending on the social needs and

composition of the species. For example, the most frequently documented social subgroup for cetaceans is mother/calf pairs, which presumably facilitates offspring survival (reviewed in Connor et al., 2000). This developmentally driven social composition substantiates the various observations that the first social-play partner for a calf is typically its mother. In contrast, adult females and males without calves would have to interact with each other for social-play opportunities, presuming other adults were around and also motivated to play. The function of adult and juvenile play may be better understood from a societal level rather than an individual level.

Transmission

Imitation during play is one way that behaviors are transmitted across the population. Behaviors can be transmitted between mothers and calves (vertical transmission), between same-aged peers (horizontal transmission), and between older and younger cetaceans (oblique transmission) (Herzing, 2005). A number of social transmission mechanisms have been identified, including different forms of imitation and teaching (Kuczaj & Yeater, 2006). Although the exact mechanisms of observational learning are still debated, strong evidence exists for social learning as a way for individuals to increase their current knowledge. Brief descriptions of the different forms of observational learning discussed in this section are provided in Table 7.

Socio-sexual play: Alliance, dominance, and the transmission of courtship behaviors Although they are often difficult to distinguish from sexual behavior, socio-sexual interactions are considered nonconceptive behaviors that occur between any age–sex class combinations, which may include copulation and genital investigation or stimulation (reviewed by Connor et al., 2000). Socio-sexual interactions are not often included in the discussion of play, but certain of these interactions can be considered playful. For example, adult female bottlenose dolphin mothers will initiate socio-sexual interactions with their calves and allow their calves to reciprocate (reviewed by Connor et al., 2000). Immature female belugas will also participate in socio-sexual interactions that involve social play (Hill, Dietrich, et al., 2015).

The majority of socio-sexual interactions are between males among bottlenose dolphin and beluga subadults and adults (reviewed by Connor et al., 2000; Glabicky et al., 2010; Hill, Dietrich, et al., 2015). Social play involving socio-sexual behaviors has also been documented between subadult and juvenile male resident killer whales (Rose, 1992) and in killer whales in managed care (H. Hill, personal observation). Among juvenile male bottlenose dolphins, socio-sexual play may indirectly function to increase reproductive fitness through the formation of male alliances and coalitions that exist as part of the social hierarchy (Connor, Heithaus, & Barre, 2001; Connor et al., 2000). Many of these alliances formed as juveniles have been observed to last into adulthood (Mann, 2006), and although some alliances are

Table 7 Learning and transmission mechanisms involving play

Type of Mechanism	Definition	Cetacean Calf Examples
Independent Learning (trial and error)	Individual performs action without prior knowledge, a model, or guidance	Locomotor activities such as buoyancy control, manipulation of various objects, including water
Stimulus enhancement	An individual is interacting with or attending an object, which draws the attention of another individual who then interacts with the object differently	Calf's mother manipulates a toy and calf seeks the toy out and begins interacting with it on its own
Local enhancement	An individual is interacting with or attending to a location, which draws the attention of another individual who then attends or seeks out the same or a similar location	Calf's mother orients in a direction or swims through a visually distinct area (e.g., seaweed/gate), and calf orients and begins to explore the same area independently
Exposure	An individual experiences an event or a stimulus because it is in the presence of a second individual performing the activity.	A calf swimming in infant position can observe the mother manipulating a piece of seaweed or a toy with her rostrum.
Contagion	An individual starts performing the same activity as another without awareness, may be reflexive/unintentional	Dolphins are leaping and other animals begin leaping
Imitation	Broadly defined, an individual performs an action that is replicated exactly or with some variation by another individual See Kuczaj and Yeater (2006) for summary of different types of imitation.	*True imitation*: Calf observes peer back breach and performs the exact same behavior for the first time *Goal emulation*: Calf observes mother pull toy off with flukes, but calf pulls toy off shelf with body
Demonstration	A model performs a behavior purposefully to an observer	Mother swims slower and moves head intentionally while hunting a fish when calf present.
Scaffolding	An expert provides guidance to assist a novice in completing a task.	Mother pulls a toy partially off the shelf so her calf can pull it off fully
Teaching	An expert guides a novice through an unfamiliar action	Mother pushes calf off of beach after calf beaches

Table descriptions are derived from Blackmore (1998); Herzing (2005); Kuczaj & Yeater (2006); Yeater & Kuczaj (2010).

based on kinship, affiliation between conspecifics is also important (Connor & Krützen, 2015).

Beyond alliance formation, recent research has indicated a potential link between male–male socio-sexual interactions and the transmission of courtship behaviors for some species of Cetacea (Hill, Dietrich, et al., 2015; Lomac-Macnair, Smultea, Cotter, Thissen, & Parker, 2015). Some degree of courtship has been observed in humpback whales, gray whales, belugas, and possibly killer whales (Baker & Herman, 1984; Everitt & Krogman, 1979; Hill, Dietrich, et al., 2015; Tyack & Whitehead, 1983). Courtship behaviors can be innate or learned and function to draw the attention of potential mates (Freeberg, 2000; Lorenz, 1958). Population-specific courtship behaviors are transmitted through social learning and directly influence reproductive success (Kirkpatrick & Dugatkin, 1994; Laland, 1994a, b). Although they are beyond the current scientific understanding of cetaceans, social learning and cultural transmission of courtship behaviors through socio-sexual play can have far-reaching implications for conservation (Wade, Reeves, & Mesnick, 2012).

Play in the transmission of specialized foraging and hunting behaviors Cetaceans are especially well known for their specialized foraging and hunting techniques. Sometimes referenced as a level of culture, these population-specific behaviors are transmitted socially between members of the community (reviewed by Rendell & Whitehead, 2001). In some populations, killer whales and other dolphins create fish balls using echolocation, tail slaps, or herding actions (Fertl & Würsig, 1995; Similä & Ugarte, 1993). Bottlenose dolphins and Irrawaddy dolphins (*Orcaella brevirostris*) have been reported cooperating with human fishermen by driving fish toward shore into the fishing nets, where the humans then allow the dolphins to access the bycatch (bottlenose dolphins: Pryor, Lindbergh, Lindbergh, & Milano, 1990; Irrawaddy dolphins: Smith, Thant, Lwin, & Shaw, 1997). Some dolphins have learned to use tools (i.e., sponges) to exploit special foraging contexts (Sargeant & Mann, 2009; Smolker et al., 1997). Independently, different populations of dolphins and several populations of killer whales have learned to beach themselves to pursue prey (e.g., mud flat dolphins: Sargeant, Mann, Berggren, & Krützen, 2005; Santos, 2010; Silber & Fertl, 1995; and killer whales in Crozets and South America: Guinet, 1991; Guinet & Bouvier, 1995; Lopez & Lopez, 1985).

Despite the various observations of unique foraging techniques, only a handful of these techniques have been observed for long enough and with enough frequency to determine their possible transmission mechanisms. Given the social nature of many of the species that demonstrate these specialized foraging techniques, it seems very likely that play becomes an important transmission device, especially for those cases involving the active guidance of immature animals (i.e., teaching, tutoring, or scaffolding; Table 7) by older, expert animals (i.e., *oblique* transmission; Herzing, 2005). Whether or not direct guidance is present, play contexts provide multiple social opportunities to learn about foraging specializations. In most cases, this may simply be a matter of exposure, as the calf is brought along for the ride while swimming with its mother. In other cases, more complex transmission methods may be used (see Table 7).

Cetaceans are also a group for which evidence for possible teaching is slowly being amassed. Adult killer whales from different populations will intentionally strand themselves in order to catch seals or sea lions (Guinet, 1991; Guinet & Bouvier, 1995; Lopez & Lopez, 1985). These killer whales appear to have apprenticeships that are oblique in nature, such that a nonmother adult female guides a calf working on the beaching behavior in a bout that can only be described as play—a seal is not necessarily present, and the calf repeatedly practices the beaching behavior using exaggerated movements (Guinet, 1991). Killer whale calves in the Crozet Archipelago initially practice intentional stranding as part of social play with an adult female (i.e., oblique transmission) or with their mother (i.e., vertical transmission) (Guinet, 1991; Guinet & Bouvier, 1995). Similarly, Herzing and her colleagues have documented apparent teaching behavior by spotted dolphin mothers while foraging with their calves (Bender et al., 2009; Herzing, 2005). Nine mother dolphins displayed significantly longer chase durations and made significantly more body-orienting movements when foraging in the presence of their calves than when foraging alone. The chase durations were particularly impressive as they were eight times longer for the female dolphins when foraging with their calves than without (presented by Bender et al., 2009).

Play in the development and transmission of novel behaviors Janik (2015) wrote, "Young animals are the main source of invention for new games and are the ones playing most often" (p. R8). As play peaks during the juvenile years, it is characterized by innovation and peer interaction. Peer play is thought to facilitate the transmission of novel behaviors throughout a social group (Greene et al., 2011; Kuczaj et al., 2006). It has been suggested that by observing peer play, one can hold a better mental representation of an individual of the same size and ability, so that it is easier to interpret and remember the behavior, as well as reproduce the behavior in the future (Yando, Seitz, & Zigler, 1978). Both of these speculations are supported by observations that juvenile bottlenose dolphins are most likely to produce novel behaviors, as well as imitate novel behavior of their peers (Jones & Kuczaj, 2014; Kuczaj et al., 2006).

It has been suggested that observation and imitation of the observed behaviors during play may facilitate the transmission of novel behaviors. Thus, constraints on social availability, such as limited social groupings with few models of various ages, may result in developmental differences in play behavior (Bender, 2012; Mackey et al., 2014). Kuczaj et al. (2006) found

that bottlenose dolphin calves will produce more novel behaviors if two or more peers are present in the environment. Similarly, it was also found that calves will produce more complex behaviors at a younger age if raised in an environment with older peers. Given these findings, the availability of social partners, and particularly exposure to older and more experienced peers, has the potential to affect the structure, amount, and behavioral diversity of play (Bender, 2012; Kuczaj et al., 2006; Mackey et al., 2014; Pellis & Pellis, 2007).

Adults are most likely to mimic calves, who seem to act as a catalyst for innovation across the population (Hill & Ramirez, 2014; Jones & Kuczaj, 2014; Kuczaj et al., 2006). Benefits of imitation include increasing behavioral repertoires and creating more models from which others can learn (Kuczaj & Eskelinen, 2014; Kuczaj et al., 2006). Evidence for this hypothesis has come from several sources. In managed care, the behavioral repertoires of adult belugas were diversified when beluga calves were present (Hill, Guarino, Crandall, Lenhart, & Dietrich, 2015). In the natural habitat, a population of dolphins in Shark Bay, Australia, developed 13 distinct foraging strategies, possibly in response to changing environmental pressures (Sargeant & Mann, 2009). Within that population, the specific foraging techniques were stable across lifespans and appeared to be passed down matrilineally. It is reasonable to assume that these specialized foraging techniques resulted from a process of innovation and transmission.

Activating play

Like laughter or yawning (Provine, Provine 1996a, b, 2005), play is often discussed in the context of contagiousness (reviewed by Held & Špinka, 2011), but this has not been studied extensively in animals. Only a handful of studies have documented this phenomenon empirically in a limited number of species (rats: Pellis & McKenna, 1992; Varlinskaya, Spear, & Spear, 1999; Japanese macaques, *Macaca fuscata*: Leca, Gunst, & Huffman, 2007; Petit, Bertrand, & Thierry, 2008; ring-tailed lemurs, *Lemur catta*: Palagi, 2009; gazelles, *Gazella cuvieri*: Gomendio, 1988). Discussed by Provine (1996a) in the contexts of laughter and yawning, contagiousness is the stimulation of motor acts from one individual to another across a group of individuals without conscious control (i.e., seeing or hearing someone laugh or yawn evokes another to laugh or yawn, respectively). Play is another context in which contagiousness emerges. The question, then, arises: how? Different mechanisms of social learning have been proposed to facilitate the contagiousness of play, including exposure, stimulus enhancement, and local enhancement (Table 7; reviewed by Blackmore, 1998; Kuczaj & Yeater, 2006; Yeater & Kuczaj, 2010).

Across cetaceans, reports abound of the stimulation of play behavior among groups. For example, leaping in dolphins is often described as beginning with a small number of animals but ending with many of the group members repeating the same or similar behaviors in a synchronous manner (e.g., Hawaiian spinner dolphins, *Stenella longirostris*: Johnson & Norris, 1994). A review of the importance of synchronizing behaviors at the group level for dolphins indicated that the functions were multifaceted, ranging from increasing awareness of threats to solidifying relationships to teaching important survival skills to young (Fellner, Bauer, & Harley, 2006). Whether such play is meant to stimulate physical activity, increase vigilance, signal a possible food source or potential danger, or increase interest in some aspect of the surrounding environment that could promote investigation, and ultimately play, is still unclear. Perhaps, more simply, older animals are influenced to engage in more playful behavior due to the observation of young animals engaging in highly arousing, energetic actions. Research with dolphins and belugas in managed care suggests that the presence of younger animals increases the amounts of object play and social play exhibited by adult animals (Hill, Guarino, et al., 2015; Hill & Ramirez, 2014; Kuczaj et al., 2006).

Final thoughts

Cetacean play has been studied empirically since the early 2000s, although observations of their play have been reported anecdotally from the first field experiences. After almost 20 years of concentrated effort, research has documented the types of play (locomotor, object, and social), the form in which play occurs (solitary and social), the objects used (organic, inorganic, man-made, and natural), and the age–sex classes involved (see the review by Kuczaj & Eskelinen, 2014). The primary goal of this article has been to reexamine the state of research on cetacean play using a top-down, deductive approach. The majority of research efforts on cetacean play have been driven by a bottom-up, inductive approach, which is typical for new fields of study. Study of play by cetaceans is a relatively young field, as compared with play among such animals as primates and humans. Yet a useful body of literature is available, albeit on a small number of cetacean species in limited settings.

We selected two theoretical frameworks that can best model cetacean play behavior and potentially guide future research toward addressing the function of cetacean play from both an individual and a group perspective. Using a combination of developmental theories (Groos's play as practice, Piaget's cognitive developmental stages, and Parten's social hierarchy of play development), we demonstrated how these theories map onto known cetacean behavior and place our current understanding of cetacean play within a larger context of physical, cognitive, social, and emotional development. This approach best explains the development of play during youth, highlighting behaviors implicated for functional use in adulthood. Developmental milestones mark healthy progression through

stages of development. Establishing species-typical standards for healthy development would provide a useful blueprint for the management and welfare of cetaceans in controlled environments. Knowledge of developmental progression can also be used to inform regulations that can protect populations in their natural habitat from deleterious stimuli during particularly sensitive periods.

Also of interest is the function of play at the societal level. Play may be a critical indicator of the overall health of cetacean societies. Our review demonstrated that in cetaceans, play facilitates alliances between animals and promotes the transmission of novel and population-specific behaviors. It is clear that young members of a population have a special role in innovation, acting as the inventors and catalysts for the transmission of new behaviors. Play through adulthood and the transmission of novel behaviors to adults increases a society's ability to adapt to environmental changes. Unfortunately, some species of social Odontocetes have not been resilient after exploitation (e.g., killer whales, sperm whales, belugas, narwhals [*Monodon monoceros*], and pilot whales [*Globicephala* sp.]). Larger adults tend to be removed from the population by hunters, leaving calves and juveniles without possibly critical models; for example, socio-sexual play between juveniles and then between same-sex pairs of sexually immature and mature animals may transmit important courtship behaviors. By removing these key models from the population, overexploitation may be unrecoverable.

We contend that play is not a frivolous topic for scientists to pursue. It has the ability to inform our understanding of cetaceans in terms of a number of concepts, including social learning, transmission mechanisms, development, unobservable cognitive skills, and critical developmental milestones. The presence, frequency, and nature of play (i.e., types of play, presence of stereotypies, and degree of behavioral diversity) appear to be reliable indicators of the current psychological and physical well-being of animals in controlled environments (see Held & Špinka, 2011, for a review). We suggest that the same measures of play could be used to evaluate the current state of welfare for cetaceans in their natural habitat, as well. Examining play behaviors in wild animals may prove to be a less expensive and invasive way to evaluate the healthy functioning, availability of resources, and stress levels of a population than the current techniques being employed (e.g., health assessment and distribution tracking). Play behaviors that are observed in multiple settings, including both the field and managed care, may elucidate the elements that are conserved across settings for different species' behavioral repertoires. These conserved behaviors may allow for insights into the function and mechanisms of play. Unraveling the mysteries of play and its importance to development and survival will be an interesting puzzle that should provide challenges and much enjoyment in the future, for the animals and the researchers alike.

Author note This article would not exist if not for the legacy of Stan Kuczaj and his continuous efforts to merge the worlds of human development and animal cognition into a cohesive and rich discipline. This article is truly a reflection of Stan's passions and love of science. We thank the Psychonomic Society for the opportunity and its support in bringing together some of the world's foremost thinkers to the same table for three days to hash out what we currently understand about the evolutionary perspective on play, through the Society's Leading Edge Series. This article has also provided a remarkable experience for H.M.H., who was afforded the opportunity to participate in the workshop and the development of this paper with Stan's unexpected passing. We hope the ideas in this article resonate with those Stan was seeking to promote when he joined forces with Lance Miller and Alex de Voogt to explore the fun yet challenging topic of what play is and what it means through the workshop. We also thank Kathleen Dudzinski for her helpful comments on a previous draft of this paper.

References

Asper, E. D., Young, W. G., & Walsh, M. T. (1988). Observations on the birth and development of a captive-born Killer whale Orcinus orca. *International Zoo Yearbook, 27,* 295–304.

Baird, R. W. (2000). The killer whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 127–153). Chicago, IL: University of Chicago Press.

Bakeman, R., & Brownlee, J. R. (1980). The strategic use of parallel play: A sequential analysis. *Child Development, 51,* 873–878.

Baker, C. S., & Herman, L. M. (1984). Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology, 62,* 1922–1937.

Baldwin, J. D., & Baldwin, J. D. (1978). The primate contribution to the study of play. In M. A. Salter (Ed.), *Anthropological perspectives* (pp. 53–68). New York, NY: Leisure Press.

Barber, T. M. (2016). Variety and use of objects carried by provisioned wild Australian humpback dolphins (*Sousa sahulensis*) in Tin Can Bay, Queensland, Australia. *International Journal of Comparative Psychology, 29,* 1–21. **Retrieved from http://escholarship.org/uc/item/8pt5z83j**

Bauer, E. B., & Smuts, B. B. (2007). Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris. Animal Behavior, 73,* 489–499.

Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *Quarterly Review of Biology, 47,* 412–434.

Bender, C. E. (2012). *Social play as a tool for developing social-cognitive skills in a wild population of Atlantic spotted dolphins (Stenella frontalis)*. Unpublished PhD thesis, Florida Atlantic University, Boca Raton, FL.

Bender, C. E., Herzing, D. L., & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition, 12,* 43–53.

Blackmore, S. (1998). Imitation and the definition of a meme. *Journal of Memetics-Evolutionary Models of Information Transmission, 2,* 159–170.

Blois-Heulin, C., Rochais, C., Camus, S., Fureix, C., Lemasson, A., Lunel, C., & Hausberger, M. (2015). Animal welfare: Could adult play be a false friend. *Animal Behavior and Cognition, 2,* 156–185.

Brooker, E., Blaise, M., & Edwards, S. (Eds.). (2014). *SAGE handbook of play and learning in early childhood*. New York, NY: Sage.

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge, MA: MIT Press, Bradford Books.

Cairns, R. B. (1976). The ontogeny and phylogeny of social interactions. In M. E. Hahn & E. C. Simmel (Eds.), *Communicative behavior and evolution* (pp. 115–139). New York, NY: Academic Press.

Chechina, O. N. (2009). Formation of behavior in bottle-nosed dolphin newborns under conditions of an oceanarium: Heterochrony of involvement of various types of afferentiation. *Biology Bulletin, 36,* 489–492.

Clapham, P. J. (2000). The humpback whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 173–196). Chicago, IL: University of Chicago Press.

Cockcroft, V., & Ross, G. J. B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 461–478). San Diego, CA: Academic Press.

Connor, R. C. (2000). Group living in whales and dolphins. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199–218). Chicago, IL: University of Chicago Press.

Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin "super-alliance". *Proceedings of the Royal Society B, 268,* 263–267.

Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Animal Behaviour, 103,* 223–235.

Connor, R. C., & Peterson, D. M. (1994). *The lives of whales and dolphins*. New York, NY: Holt.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–125). Chicago, IL: University of Chicago Press.

de Vere, A. J., & Kuczaj, S. A. (2016). Where are we in the study of animal emotions? *Wiley Interdisciplinary Reviews: Cognitive Science, 7,* 354–362.

Deakos, M. H., Branstetter, B. K., Maxxuca, L., Fertl, D., & Mobley, J. R. (2010). Two unusual interactions between a bottlenose dolphin (*Tursiops truncatus*) and a humpback whale (*Megaptera noraeangliae*) in Hawaiian waters. *Aquatic Mammals, 36,* 121–128.

Deutsch, S., Pearson, H., & Würsig, B. (2014). Development of leaps in dusky dolphin (*Lagenorhynchus obscurus*) calves. *Behaviour, 151,* 1555–1577.

Dibble, D. S., Van Alstyne, K. R., & Ridgway, S. (2016). Dolphins signal success by producing a victory squeal. *International Journal of Comparative Psychology, 29,* 1–10. **Retrieved from http://escholarship.org/uc/item/89w2680r**

Dietrich, S., Garza, S., Hill, H., & Aibel, S. (2013, July). *Oral exploratory interaction:* "*The mouth game*"*—A developmental precursor to aggressive threats or courting behavior?* Paper presented at the Animal Behavior Society Meeting (ABS), Boulder, CO.

Everitt, R. D., & Krogman, B. D. (1979). Sexual behavior of bowhead whales observed off the north coast of Alaska. *Arctic, 32,* 277–280.

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

Fagen, R. (1995). Animal play, games of angels, biology and brain. In A. D. Pellegrini (Ed.), *The future of play theory*. Albany, NY: New York University Press.

Félix, F. (2015). Rope rubbing social play behavior recorded from wild bottlenose dolphins (*Tursiops truncatus*) in Ecuador. *Aquatic Mammals, 41,* 222–225.

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

Fertl, D., & Würsig, B. (1995). Coordinated feeding by Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico. *Aquatic Mammals, 21,* 3–5.

Freeberg, T. M. (2000). Culture and courtship in vertebrates: A review of social learning and transmission of courtship systems and mating patterns. *Behavioural Processes, 51,* 177–192.

George, E. M., & Noonan, M. (2016). Underwater bubbling in beluga whales (*Delphinapterus leucas*): Rates of production as a function of age, sex, and bubble type. *Integrative and Comparative Biology, 56*, E290–E290.

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

Glabicky, N., DuBrava, A., & Noonan, M. (2010). Social–sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). *Polar Biology, 33,* 1145–1147.

Goldman, J. A. (1981). Social participation of preschool children in same- versus mixed-age groups. *Child Development, 52,* 644–650.

Gomendio, M. (1988). The development of different types of play in gazelles: implications for the nature and functions of play. *Animal Behaviour, 36*, 825–836.

Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology, 24,* 292–306.

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

Groos, K. (1901). *The play of man*. London, UK: Heinemann.

Guarino, S., Hill, H. M., & Sigman, J. (2016). Development of sociality and emergence of independence in a killer whale (*Orcinus orca*) calf from birth to 36 months. *Zoo Biology, 36,* 11–20.

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.

Hausberger, M., Fureix, C., Bourjade, M., Wessel-Robert, S., & Richard-Yris, M. A. (2012). On the significance of adult play: What does social play tell us about adult horse welfare? *Naturwissenschaften, 99,* 291–302.

Held, S. D., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour, 81,* 891–899.

Herzing, D. L. (2005). Transmission mechanisms of social learning in dolphins: Underwater observations of free-ranging dolphins in the Bahamas. In F. Delfour & M. J. Dubois (Eds.), *Autour de l'ethologie et de la cognition animale* (pp. 185–193). Lyon, France: 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,* 85–99.

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

Highfill, L. E., Yeater, D., & Kuczaj, S. A., II. (2016). Catch! Dolphin (*Tursiops truncatus*) ball tossing to humans is affected by human perspective. *Aquatic Mammals, 42,* 253–258.

Hill, H. M. (2009). The behavioral development of two beluga calves during the first year of life. *International Journal of Comparative Psychology, 22,* 234–253.

Hill, H. M., Kahn, M. S., Brilliott, L. J., Roberts, B. M., Gutierrez, C., & Artz, S. (2011). Beluga (*Delphinapterus leucas*) Bubble bursts: Surprise, protection, or play?. *International Journal of Comparative Psychology, 24*, 235–243.

Hill, H. M., Campbell, C., Dalton, L., & Osborn, S. (2013). The first year of behavioral development and maternal care of beluga (*Delphinapterus leucas*) calves in human care. *Zoo Biology, 32,* 565–570.

Hill, H. M., Dietrich, S., Yeater, D., McKinnon, M., Miller, M., Aibel, S., & Dove, A. (2015). Developing a catalog of socio-sexual behaviors

of beluga whales (*Delphinapterus leucas*). *Animal Behavior and Cognition, 2,* 105–123.

Hill, H., Guarino, S., Crandall, S., Lenhart, E., & Dietrich, S. (2015). Young belugas diversify adult beluga (*Delphinapterus leucas*) behavior. *Animal Behavior and Cognition, 2,* 267–284.

Hill, H., & Ramirez, D. (2014). Adults play but not like their young: The frequency and types of play by belugas (*Delphinapterus leucas*) in human care. *Animal Behavior and Cognition, 1,* 166–185.

Hill, H. M., Yeater, D., Gallup, S., Guarino, S., Lacy, S., Dees, T., & Kuczaj, S. (2016). Responses to familiar and unfamiliar humans by belugas (*Delphinapterus leucas*), bottlenose dolphins (*Tursiops truncatus*), & Pacific white-sided dolphins (*Lagenorhynchus obliquidens*): A replication and extension. *International Journal of Comparative Psychology, 29,* 1–21. **Retrieved from http://escholarship.org/uc/item/48j4v1s8**

Hughes, C., & Leekam, S. (2004). What are the links between theory of mind and social relations? Review, reflections and new directions for studies of typical and atypical development. *Social Development, 13,* 590–619.

Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., & Trone, M. (2010). What do dolphins (*Tursiops truncatus*) understand about hidden objects? *Animal Cognition, 13,* 103–120.

Janik, V. M. (2015). Play in dolphins. *Current Biology, 25,* R7–R8.

Johnson, C. M., & Norris, K. S. (1994). Social behavior. In K. S. Norris, B. Würsig, R. S. Wells, & M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 243–286). Berkeley, CA: University of California Press.

Johnson, C. M., Sullivan, J., Buck, C. L., Trexel, J., & Scarpuzzi, M. (2015). Visible and invisible displacement with dynamic visual occlusion in bottlenose dolphins (*Tursiops* sp. *Animal Cognition, 18,* 179–193.

Jones, B., & Kuczaj, S. A. (2014). Beluga (*Delphinapterus leucas*) novel bubble helix play behavior. *Animal Behavior and Cognition, 1,* 206–214.

Kilborn, S. S. (1994). Object carrying in a captive beluga whale (*Delphinapterus leucas*) as possible surrogate behavior. *Marine Mammal Science, 10*, 496–501.

Kirkpatrick, M., & Dugatkin, L. A. (1994). Sexual selection and the evolutionary effects of copying mate choice. *Behavioral Ecology and Sociobiology, 34,* 443–449.

Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., & Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (*Delphinapterus leucas*) in natural environment. *Biology Bulletin, 41,* 349–356.

Kuczaj, S. A., & Eskelinen, H. C. (2014). Why do dolphins play? *Animal Behavior and Cognition, 1,* 113–127.

Kuczaj, S. A., & Frick, E. E. (2015, December). *What do dolphins mean when they open their mouth?* Poster presented at the meeting of the Society for Marine Mammalogy, San Francisco, CA.

Kuczaj, S. A., & Highfill, L. E. (2005). Dolphin play: Evidence for cooperation and culture. *Behavioral and Brain Sciences, 28,* 405–406.

Kuczaj, S. A., II, & Horback, K. M. (2012). Play and emotion. In S. Watanabe & S. Kuczaj (Eds.), *Emotions of animals and humans* (pp. 87–112). Tokyo, Japan: Springer Japan.

Kuczaj, S. A., II, & 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: MIT Press.

Kuczaj, S. A., II, 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., Tranel, K., Trone, M., & Hill, H. (2001). Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. *Animal Welfare, 10,* S161–S174.

Kuczaj, S. A., II, Winship, K. A., & Eskelinen, H. C. (2015). Can bottlenose dolphins (*Tursiops truncatus*) cooperate when solving a novel task? *Animal Cognition, 18,* 543–550.

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

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

Laland, K. N. (1994a). A theoretical investigation of the role of social transmission in evolution. *Ethology and Sociobiology, 13,* 87–113.

Laland, K. N. (1994b). On the evolutionary consequences of sexual imprinting. *Evolution, 48,* 477–489.

Leca, J. B., Gunst, N., & Huffman, M. A. (2007). Age-related differences in the performance, diffusion, and maintenance of stone handling, a behavioral tradition in Japanese macaques. *Journal of Human Evolution, 53,* 691–708.

Lillard, A. S. (2015). The development of play. In L. S. Liben & U. Mueller (Eds.), *Handbook of child psychology and developmental science processes* (7th ed., Vol. 2, pp. 425–468). New York, NY: Wiley-Blackwell.

Lomac-Macnair, K. S., Smultea, M. A., Cotter, M. P., Thissen, C., & Parker, L. (2015). Socio-sexual and probable mating behavior of Cook Inlet beluga whales, *Delphinapterus leucas*, observed from an aircraft. *Marine Fisheries Review, 77,* 32–40.

Lopez, J. C., & Lopez, D. (1985). Killer whales (*Orcinus orca*) and their behavior of intentional stranding while hunting nearshore. *Journal of Mammalogy, 66,* 181–183.

Lorenz, K. Z. (1958). The evolution of behavior. *Scientific American, 199,* 67–78.

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.

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M., & Siegel, J. M. (2008). Cetacean sleep: An unusual form of mammalian sleep. *Neuroscience & Biobehavioral Reviews, 32,* 1451–1484. doi:10.1016/j.neubiorev.2008.05.023

Mackey, A. D., Makecha, R. N., & Kuczaj, S. A., II. (2014). The development of social play in bottlenose dolphins (*Tursiops truncatus*). *Animal Behavior and Cognition, 1,* 19–35.

Mann, J. (2006). Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In V. Sommer & P. L. Vasey (Eds.), *Homosexual behaviour in animals* (pp. 107–130). Cambridge, UK: Cambridge University Press.

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

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.

Mason, W. A. (1968). Early social deprivation in the nonhuman primates: Implications for human behavior. In D. C. Glass (Ed.), *Environmental influence* (pp. 70–101). New York, NY: Rockefeller University Press and Russell Sage Foundation.

McBride, A., & Kritzler, H. (1951). Observations of pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammalogy, 32,* 251–266.

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,* 98–106.

Mitchell, R. W. (1990). A theory of play. *Interpretation and Explanation in the Study of Animal Behavior, 1,* 197–227.

Noren, S. R., Biedenbach, G., & Edwards, E. F. (2006). Ontogeny of swim performance and mechanics in bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology, 209,* 4724–4731.

Norris, K. S., Wursig, B., & Wells, R. S. (1994). The spinner dolphin. In K. S. Norris, B. Wursig, R. S. Wells, & M. Wursig (Eds.), *The Hawaiian spinner dolphin*. Berkeley, CA: University of California Press.

Osvath, M., & Sima, M. (2014). Sub-adult ravens synchronize their play: A case of emotional contagion. *Animal Behaviour and Cognition, 1,* 197–205.

Owen, K., Dunlop, R., & Donnelly, D. (2012). Seaweed interactions by humpback whales (*Megaptera novaeangliae*): A form of object play? *Aquatic Mammals, 38,* 418–422.

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

Pack, A. A., & Herman, L. M. (2004). Bottlenose dolphins (*Tursiops truncatus*) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology, 118,* 160–171.

Palagi, E. (2009). Adult play fighting and potential role of tail signals in ringtailed lemurs (*Lemur catta*). *Journal of Comparative Psychology, 123,* 1–9. doi:10.1037/0735-7036.123.1.1

Palagi, E., Burghardt, G. M., Smuts, B., Cordoni, G., Dall'Olio, S., Fouts, H. N., & Pellis, S. M. (2016). Rough-and-tumble play as a window on animal communication. *Biological Reviews, 91,* 311–327.

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

Paulos, R. D., Trone, M., & Kuczaj, S. A. (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology, 23,* 701–722.

Pearson, H. C. (2017). Unravelling the function of dolphin leaps using the dusky dolphin (*Lagenorhynchus obscurus*) as a model species. *Behaviour, 154,* 563–581.

Pellis, S. M., & McKenna, M. (1992). Intrinsic and extrinsic influences on play fighting in rats: Effects of dominance, partner playfulness, temperament and neonatal exposure to testosterone propionate. *Behavioral and Brain Sciences, 50,* 135–145.

Pellis, S., & Pellis, V. (2007). Rough-and-tumble play and the development of the social brain. *Current Directions in Psychological Science, 16,* 95–98.

Petit, O., Bertrand, B., & Thierry, B. (2008). Social play in crested and Japanese macaques: Testing the covariation hypothesis. *Journal of Developmental Psychobiology, 50,* 399–407.

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

Provine, R. R. (1996a). Contagious yawning and laughter: Significance for sensory feature detection. In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture* (p. 179-208). Academic Press: San Diego.

Provine, R. R. (1996a). Laughter. *American Scientist, 84,* 38–45.

Provine, R. R. (2005). Yawning: The yawn is primal, unstoppable and contagious, revealing the evolutionary and neural basis of empathy and unconscious behavior. *American Scientist, 93,* 532–539.

Pryor, K. W., Lindbergh, J., Lindbergh, S., & Milano, R. (1990). A dolphin-human fishing cooperative in Brazil. *Marine Mammal Science, 6,* 77–82.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences, 24,* 309–324.

Rose, N. (1992). The social dynamics of male killer whales, *Orcinus orca* (Doctoral dissertation). British Columbia University.

Santos, M. C. D. O. (2010). Guiana dolphins (*Sotalia guianensis*) displaying beach hunting behavior in the Cananéia estuary, Brazil: Social context and conservation issues. *Brazilian Journal of Oceanography, 58,* 143–152.

Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour, 78,* 715–721.

Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behaviour, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology, 83,* 1400–1410.

Silber, G. K., & Fertl, D. (1995). Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River Delta, Mexico. *Aquatic Mammals, 21,* 183–186.

Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in Northern Norway. *Canadian Journal of Zoology, 71,* 1494–1499.

Smith, B. D., Thant, U. H., Lwin, J. M., & Shaw, C. D. (1997). Investigation of cetaceans in the Ayayarwady River and northern coastal waters of Myanmar. *Asian Marine Biology, 14,* 173–94.

Smolker, R. A., Richards, A. F., Connor, R. C., Mann, J., & Berggren, P. (1997). Sponge-carrying by Indian Ocean bottlenose dolphins: Possible tool-use by a delphinid. *Ethology, 103,* 454–65.

Spencer, H. (1873). *The principles of psychology.* Appleton: New York.

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

Thieltges, H., Lemasson, A., Kuczaj, S., Böye, M., & Blois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Animal Cognition, 14,* 303–308. doi:10.1007/s10071-010-0354-5

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

Tschudin, A. J. (2001). "Mindreading" mammals? Attribution of belief tasks with dolphins. *Animal Welfare, 10,* 119–127.

Tyack, P., & Whitehead, H. (1983). Male competition in large groups of wintering humpback whales. *Behaviour, 83,* 132–154.

Varlinskaya, E. I., Spear, L. P., & Spear, N. E. (1999). Social behavior and social motivation in adolescent rats: Role of housing conditions and partner's activity. *Physiology & Behavior, 67,* 475–482.

Wade, P. R., Reeves, R. R., & Mesnick, S. L. (2012). Social and behavioural factors in cetacean responses to overexploitation: Are Odontocetes less "resilient" than Mysticetes? *Journal of Marine Biology, 2012*(567276), 1–15. doi:10.1155/2012/567276

Weaver, A., & Kuczaj, S. (2016). Neither toy nor tool: Grass-wearing behavior among free-ranging bottlenose dolphins in Western Florida. *International Journal of Comparative Psychology, 29,* 1–18. **Retrieved from http://escholarship.org/uc/item/893417x3**

Whitehead, A. N. (1985). *Symbolism: Its meaning and effect*. New York, NY: Fordham University Press.

Würsig, B., & Würsig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fisheries Bulletin, 77,* 871–890.

Yando, R., Seitz, V., & Zigler, E. (1978). *Imitation: A developmental perspective*. Hillsdale, NJ: Erlbaum.

Yeater, D., & Kuczaj, S. (2010). Observational learning in wild and captive dolphins. *International Journal of Comparative Psychology, 23,* 379–385.