International Journal of Comparative Psychology, 2010, 23, 538-565.

The Synergy of Laboratory and Field Studies of Dolphin Behavior and Cognition

Adam A. Pack
University of Hawai'i at Hilo, U.S.A.
The Dolphin Institute, U.S.A.

Dolphin behavior and cognition have been studied in both the laboratory and the wild. Laboratory studies provide high levels of control over experimental variables and the opportunity to investigate the cognitive mechanisms of behavior. However, laboratory studies are typically limited to a few subjects. Field studies have the benefit of examining behavior and social interactions among large numbers of individuals. They can reveal how cognitive abilities are expressed naturally, and can provide external validity for observations in the laboratory. However, there is typically less control over experimental variables in field studies than in the laboratory. Thus, a synergistic relationship has emerged between laboratory and field studies of dolphin behavior and cognition with each contributing information and ideas to the other that can lead to new questions and insights. This relationship is demonstrated using four issues: a) the types of percepts and mental representations dolphins can form through echolocation; b) the complexity of relationships that dolphins can understand; c) the dolphin's competency in symbolic referential communication; and d) the dolphin's ability to manage joint attention through pointing and gazing.

In many areas of animal behavior, a synergistic relationship develops between laboratory and field studies, each contributing information and ideas to the other that can lead to new questions and insights (e.g., Balda, Pepperberg, & Kamil, 1998; de Waal & Tyack, 2003). This is especially useful because laboratory and field studies often emphasize different aspects of behavior. Laboratory studies provide high levels of control over experimental variables and offer the opportunity to investigate the foundations and mechanisms of behavior. However, studies are typically limited to a few subjects. Field studies have the benefit of examining behavior and social interactions among larger numbers of individuals. They can provide insight into how behavioral mechanisms revealed in the laboratory are expressed in natural settings, and can provide external validity for behavioral observations in the laboratory. However, there is typically less control over experimental variables than in the laboratory.

Usually, findings from the laboratory alone or the field alone are not sufficient to fully describe an area of animal behavior. Rather, it is the synthesis of findings from both the laboratory and field that provides the most complete and compelling description of animal behavior including its underlying mechanisms

Much of the work summarized in this paper was carried out at the Kewalo Basin Marine Mammal Laboratory in Honolulu. These studies were supported by grants from Earthwatch, the National Science Foundation, the Office of Naval Research, the LeBurta Atherton Trust and by contributions to The Dolphin Institute. I thank all the staff, students, and volunteers that participated in these studies. I am grateful to the two anonymous reviewers whose comments were helpful to me in revising the original manuscript. Correspondence concerning this article should be addressed to Adam A. Pack Department of Psychology University of Hawai'i at Hilo, 200 West Kawili Street, Hilo, Hawai'i 96720, U.S.A. (pack@hawaii.edu).

and functions. The synthesis of findings from laboratory and field research has proven particularly helpful in understanding animal cognition (see Tomasello & Call, 1997 for studies of primate cognition). An animal's cognitive characteristics (i.e., its cognitive abilities, specializations, and limitations, after Herman, 1980) may be best suited for study in the laboratory where conditions and variables may be carefully controlled and where subjects may be trained and tested in particular tasks (e.g., Herman, Pack, & Morrel-Samuels, 1993; Savage-Rumbaugh, 1986). Alternatively, the expression of an animal's cognitive abilities (i.e., the natural behaviors, social interactions, and communications that reflect underlying cognitive structures and mechanisms) may be best studied in the wild (e.g., Cheney & Seyfarth, 1990).

The synergistic relationship between laboratory and field studies in animal cognition was recognized early by some researchers studying dolphin cognition (e.g., Herman, 1980), and has subsequently inspired symposia (e.g., Pack & Herman, 1993) and documentary films (e.g., British Broadcasting Company, 2003) that emphasize this synergy. Nonetheless, some continue to question the usefulness of studies of captive dolphins in understanding dolphin behavior and cognition (Rose, Parsons, & Farinato, 2009). In this paper, I compare laboratory and fieldwork approaches in the study of dolphin behavior and cognition[1], describe how studies using one approach have influenced studies using the other, and then discuss how the synthesis of findings using both approaches has been useful in understanding four topics in dolphin cognition: dolphin perception through echolocation, dolphin understanding of complex relationships, dolphin understanding of referential symbolic communication, and dolphin understanding of management of joint attention. For each of these topics, laboratory evidence is presented first followed by field evidence, and finally synthesis[2].

Table 1 compares the general methods of laboratory and field studies of dolphin behavior and cognition. Laboratory studies typically involve one or a few subjects living within habitats that are limited in size. They provide excellent opportunities for observing behaviors above and below the water surface. Field studies typically canvas expansive habitats and home ranges containing groups and communities of dolphins. Both methods involve gathering data at the level of the individual but often in different ways and for different purposes. An overall virtue of laboratory studies is the ultimate control they provide over a wide variety of variables. Although some laboratory studies passively survey the behavior and communication of dolphins (e.g., Highfill & Kuczaj, 2007; Killebrew, Mercado, Herman, & Pack, 2001; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; McCowan & Reiss, 1995a, b, c; Perelberg & Schuster, 2008, 2009; Reiss & Marino, 2001), many others focus on training dolphins to perform behavioral tasks that enable tests of their cognitive characteristics (Herman, 1980). Typically, stimuli used in cognitive tests are not limited to those found in the dolphin's natural world.

---

[1] Unless otherwise noted, "dolphin" refers to bottlenose dolphin (*Tursiops* sp.).

[2] This order does not necessarily represent the chronological order of studies. For instance in many cases, early findings from the wild influenced later studies in the laboratory.

Arbitrary stimuli and abstract symbols are often employed in order to examine the breadth of cognitive ability and cognitive potential. These types of methods have been used successfully to directly investigate specific topics in dolphin cognition such as rule learning, concept formation, mental representations, memory systems, imitation, comprehension of social cues, and language abilities (see reviews in Herman, 1980, 2002, 2006; Herman Pack & Morrel-Samuels, 1993; Herman, Pack & Wood, 1994; Marino et al., 2007; Pack & Herman, 2006; Pack, Herman & Hoffmann-Kuhnt, 2004). However, the latter types of studies often require a considerable investment of time and effort in the training of individual dolphins. The dividend of this investment is a "well-schooled" individual with a foundation of knowledge, skills, and problem-solving strategies that can be used to investigate complex areas of cognition (Herman, Pack et al., 1993).

In contrast to laboratory methods for studying dolphin behavior and cognition, field studies of these topics often begin with the *identification* of individual dolphins and the compilation of their associations, individual life histories and social networks. Although formal field experiments on dolphin behavior and cognition may be conducted in the wild (e.g., Sayigh et al., 1999), often what is emphasized is the passive observation of behaviors, associations, social interactions and communication events. This information provides a high level of external validity for passive observations of dolphin behavior in the laboratory, and also provides insights into how dolphin cognition is expressed in the wild amidst changing environmental and social pressures (e.g., Connor & Mann, 2006).

In summary, there are many substantial differences between the methods used and the types of results that may be obtained in laboratory studies and field studies of dolphin behavior and cognition. Despite these differences, findings from the laboratory and field are often complimentary. Researchers studying dolphins in the laboratory often access the findings of researchers studying dolphins in the wild to understand how the behaviors and cognitive abilities revealed in the laboratory may manifest themselves in the dolphin's natural world as well as what environmental and/or social pressures may have lead to the selection of particular cognitive characteristics (e.g., Herman, 1980; Pack & Herman, 2006). Conversely, researchers studying dolphins in the wild often access the findings of researchers studying dolphins in the laboratory to better understand the cognitive processes and mechanisms that may underlie the behaviors and social interactions they are observing in wild dolphins (e.g., Bender, Herzing, & Bjorklund, 2008; Tyack, 2003). This type of synergistic relationship is illustrated in the following four examples.

Table 1

Comparison of methods between laboratory studies and field studies of dolphin behavior and cognition.

General area	**Topic**	**Laboratory studies**	**Field Studies**
Subjects	Number and experience	Typically one or a few subjects (e.g., Herman, Pack et al., 1993); family history may be known; relatedness can be determined through observation and genetics; experience with experimental apparatus, stimuli and conspecifics can be either passively observed or manipulated	Typically N is greater than in laboratory studies but varies (e.g., N = 18 in Bender et al., 2008; N > 100 Connor & Mann, 2006); family histories determined through tracking individuals; relatedness can be determined through observation and genetics; experience with natural stimuli and conspecifics is typically passively observed
Habitat	Type	Pools, sea pens, lagoons (typically < 0.015 km^2, e.g., Perelberg & Schuster, 2008)	Natural open ocean, coastal, banks, inlets (home ranges typically > 100 km^2 e.g., Connor et al., 2000)
Materials	Stimuli	Often synthetic, abstract and arbitrary but may be natural as well; stimuli may serve as symbols	Most often natural; determined by dolphins through their natural interactions
Procedures	Passive type	Passive observation either without manipulation or under experimental conditions (e.g., exposure to mirror image, Reiss & Marino, 2001)	Passive observation either without manipulation or under experimental conditions (e.g., playback, Sayigh et al., 1999)
	Training	Training by humans using stimuli and principles of conditioning and reinforcement, as well as innovative communication techniques (e.g., pointing or modeling); testing with novel stimuli and/or conditions (e.g., Herman et al., 1984; Pack & Herman, 2004, 2006)	Training by humans usually does not occur
	Designs	Experimental designs usually involving manipulation of one or more variables; strong control over variables	Usually sampling behavior, social interactions, and communication; some experimental designs (e.g., playback) with control over variables
Measurements		In passive studies, measurements of behaviors, associations, and social interactions, as well as reactions to presented stimuli (e.g., auditory evoked potentials, Nachtigall, Supin, Pawloski & Au, 2004) ; In active studies, determining cognitive processes, mechanisms, and potentials by measuring performance accuracy in training and test trials, as well as discrimination judgments in tasks of perception	Determining identities of individuals and measuring degrees of association, behavior of individuals, and social interactions; measuring reactions to presented stimuli (e.g., in playback studies, Sayigh et al. 1999, or auditory evoked potential studies, Nachtigall et al. 2008); infering cognitive processes and abilities from observed behavior

Dolphin Object Perception through Echolocation

Evidence from the laboratory

In the 1940s and 50s, dolphin echolocation was discovered using captive dolphins (e.g., Kellogg & Kohler, 1952; McBride, 1956). A multitude of laboratory studies followed over the next four decades revealing that dolphins have a well-developed and sophisticated sense of echolocation (see Au, 1993 for a review). In the 1980s, a series of echolocation studies were performed with dolphins in the laboratory that focused on the dolphins' ability to discriminate object shapes using echolocation. In these studies, dolphins were typically blindfolded with removable latex eyecups to prevent the use of vision and trained to remain stationary (e.g., in a vertically suspended hoop) so that precise acoustic measurements could be obtained of echolocation signals (see Au, 1993). Using this technique, researchers demonstrated that dolphins could be trained to use echolocation to discriminate between simple shapes such as cylinders versus spheres (Au, Schusterman, & Kersting, 1980), cylinders versus cubes (Nachtigall, Murchison, & Au, 1980), and flat circles versus either flat triangles or squares (Barta, 1969, cited in Au, 1993). The basis for these discriminations was explained in terms of one or more acoustic cues present in the backscatter information from the objects (e.g., differences in highlight structure, amplitude, spectral content) (Au, 1993). The possibility that the dolphin formed a direct shape percept through echolocation (i.e., directly perceived the spatial features and structure of the object) was not considered nor did the methods used in these studies allow for determining this possibility (see Pack & Herman, 1995).

In the 1990s, Pack and colleagues began a series of new studies to examine how dolphins perceive and mentally represent objects inspected through echolocation. Herman and Pack (1992) developed a novel method using a cross-modal task to examine whether dolphin echolocation may directly yield a shape percept of an object. The cross-modal task allowed them to ask whether a shape inspected through echolocation alone could be matched to an identical shape inspected through vision alone and vice versa. Pack and Herman (1995) hypothesized that if associative learning were eliminated, by examining first-trial (i.e., spontaneous) recognition performance using a variety of novel objects that differed in shape alone, then accurate matching must reflect the dolphin's ability to form a shape percept through echolocation. That is, inasmuch as the raw physical stimuli arising from echoes and those arising from reflected light differ and are not directly correlated, first-trial matching across the senses of vision and echolocation can only be based on matching mental representations that preserve the spatial structure of the objects (i.e., mental representations that are object-based). A dolphin learning to associate particular echoes with particular objects cannot explain first-trial cross-modal matching.

To limit object inspection to vision alone, objects were held in air, a medium in which dolphin echolocation is ineffective (see Pack & Herman, 1995).

To limit object inspection to echolocation alone, objects were presented within a sound attenuation box filled with seawater and suspended underwater from poolside. A thin sheet of opaque black Plexiglas fronted the box. The Plexiglas allowed sound but not light to penetrate. Thus, a dolphin swimming up to the box could examine an object suspended inside using echolocation but not vision (see Pack & Herman, 1995 for box images and further details). These two methods for exposing objects to either vision alone or echolocation alone yielded two cross modal matching tasks. In echolocation to vision (E-V) matching, a sample object was presented inside the sound attenuation box for echolocation inspection followed by two alternative objects held in air for visual inspection. One of the alternatives matched the sample in the box. After inspecting the object in the box using echolocation, the dolphin visually searched the alternatives and stationed in front of the one that matched the sample. In vision to echolocation (V-E) matching, a sample object was held in air for the dolphin to inspect visually. Following this, each of two alternative objects was placed in its own sound attenuation box (along with two acoustic “masking” objects that were quickly withdrawn). The dolphin’s task was to press a paddle on the box containing the object that matched the sample. Note that unlike earlier studies (see Au, 1993) in which an echolocating dolphin was typically fixed in position and wore opaque eyecups, in the cross-modal studies the dolphin was allowed to swim freely during echolocation and was not required to wear eye cups. These modifications better approximated the behavior of echolocating dolphins in the wild (e.g., Herzing, 1996).

Pack et al. (2004) summarized the results of their cross-modal studies. They found that a dolphin could spontaneously (i.e., on the first trial) match complexly shaped objects across the senses of vision and echolocation in both V-E and E-V, including novel objects that had never been exposed previously to echolocation or vision. Combining the data of Pack and Herman (1995) and Herman, Pack and Hoffmann-Kuhnt (1998), a total of 26 unique objects were tested cross-modally, 24 of 26 in E-V and all 26 in V-E. The dolphin correctly matched objects across the senses on 19 of 24 first trials in E-V and 21 of 26 trials in V-E ($p < .005$ for both tests, cumulative binomial test). These findings strongly support the theory that dolphins directly perceive object shape through echolocation.

In other work, Harley, Putman, and Roitblat (2003) provided additional evidence for the direct perception of object shape through echolocation. These researchers also used a cross-modal task to examine dolphin echolocation perception but with a different methodology from Pack and colleagues. With some sets of objects, the dolphin was rewarded for selecting an alternative that physically matched the sample (as in the studies of Pack and colleagues). With other sets, however, a choice of a consistent non-matching alternative was rewarded even though a match was present among the three alternatives. Harley et al. (2003) reasoned that if the dolphin is directly perceiving shape characteristics through echolocation, then the former task should be easier for the dolphin than the latter because only in the former task is shape consistent from sample to rewarded alternative. If, however, the dolphin is simply associating sounds (echoes) with the sights of objects, then the tasks should be of equivalent difficulty (i.e., it should not matter whether or not the alternative physically matches the sample). Despite the differences in reward contingency, the dolphin tended to select the object that matched the *shape* of the sample leading Harley et al. (2003) to conclude that dolphins perceive object features directly through echolocation. However, objects do not appear to be identified simply by the perception of a single feature. In a cross-modal task using objects with overlapping features and a response paddle that the dolphin learned to use to indicate that none of the offered alternatives matched the sample, Pack, Herman, Hoffmann-Kuhnt, and Branstetter (2002) provided evidence that dolphins perceive objects through echolocation holistically.

Finally, dolphins appear to be able to take advantage of the information derived from each other's echolocation activity. Xitco and Roitblat (1996), used a pair of dolphins in an echolocation task. The first dolphin was allowed to produce echolocation signals on an object that could not be perceived visually while the second dolphin listened to the echolocation emissions of the first dolphin, as well as the echoes from the object. Xitco and Roitblat showed that the "listener" dolphin was accurate in identifying the object ensonified by the dolphin producing the echolocation signals. That is, the listener gleaned information about object identity by eavesdropping on the other dolphin's echolocation activity.

Evidence from the wild

In theory, the dolphin's ability to directly perceive the spatial structure of objects through echolocation (as demonstrated in the laboratory) may be useful in the wild in the discrimination of any physical object (e.g., prey, predator, environmental structure), especially in those instances in which visual and passive acoustic cues are absent. To date, the expression of dolphin echolocation shape perception in the wild has been most clearly observed in foraging situations in which dolphins cannot see prey visually but must rely on echolocation for their discrimination. For example, species such as spinner dolphins (*Stenella longirostris*) (Norris, Wursig, Wells, & Wursig, 1994) and Atlantic spotted dolphins (*Stenella frontalis*) (Herzing, 1996) forage at night where light is severely attenuated and vision is of limited or no use compared to echolocation. Likewise, Herzing and colleagues have shown that Atlantic spotted dolphins and bottlenose dolphins use echolocation to locate different species of eels and fish buried in the sandy bottom or hidden under ledges or in holes where visual detection and discrimination of prey is unavailable (Herzing, 2004; Rossbach & Herzing, 1997). In her summary of the nonsocial uses of dolphin echolocation in the wild, Herzing (2004) denotes two phases of echolocation behavior during foraging, a search phase, during which echolocation click rates are relatively slow (< 200 Hz) and the dolphins move their bodies and heads in conjunction with their echolocation signals, followed by an approach phase (after target detection) in which click rates increase up to 500 Hz in conjunction with the dolphin orienting with its rostrum tip into the sandy bottom and using it to dig out prey.

In these examples, the direct perception of object shape through echolocation is advantageous to the extent that prey item shape must be discriminated echoically from other shapes in the environment. The success of the dolphins foraging for a variety of mobile prey in environmental conditions in which echolocation is heavily if not exclusively relied upon suggests an echolocation perception system that has been selected for that provides an appreciation of the spatial structure of echolocated objects, as has been proposed for bats (e.g., Simmons, 1989) and as has been demonstrated with dolphins in the laboratory (e.g., Harley et al., 2003; Pack & Herman, 1995).

Synthesis

Both laboratory studies and field studies on dolphin echolocation perception have benefited from each other. For example, in the laboratory the development of an echolocation task by Pack and colleagues in which a dolphin was free to move while echolocating and was not required to wear eye cups (e.g., Pack & Herman, 1995) was developed to better model the dolphin's natural behavior while echolocating in the wild (e.g., Herzing, 1996; Rossbach & Herzing, 1997). Conversely, considerations of dolphin echolocation behavior in the wild (e.g., Herzing, 2000) have used information from laboratory studies of dolphin cross-modal abilities (Pack & Herman, 1995) and abilities to eavesdrop on the echolocation behavior of another dolphin to identify objects (Xitco & Roitblat, 1996), to better interpret echolocation behavior observed in the wild. Also, laboratory studies of dolphin echolocation signal characteristics (Au, 1993) have inspired field studies of signal characteristics of dolphins echolocating in the wild for example while engaged in foraging activities (Au & Herzing, 2003). Importantly, these latter studies have provided external validity for the types of echolocation signal measurements obtained in the laboratory.

Taken together, laboratory and field studies of dolphin echolocation are consistent with a theory of "echo-imaging" (Pack & Herman, 1995). This theory states that echolocation directly yields a shape percept of an object, and that the mental representation of an object perceived through echolocation is functionally equivalent to the representation formed through vision (i.e., it preserves information about the spatial features and structure of the object). Furthermore, the dolphin's echolocation and visual perceptual systems are integrated at the representational level. The exact mechanism underlying the formation of shape percepts through echolocation remains speculative and warrants further study (see Herman et al., 1998 for a discussion of possible mechanisms). Recent laboratory work revealing the use of a simultaneous double click echolocation mechanism in Beluga whales (*Delphinapterus leucas*) (Lammers & Castellote, 2009), and recent field work showing the functional use of echolocation by foraging Hawaiian spinner dolphins (Benoit-Bird & Au, 2009) shows the importance of continuing both laboratory and field inquiries into dolphin echolocation in the future.

Dolphin Understanding of Complex Relationships

Evidence from the laboratory

Judgments of physical similarity. The ability to understand and judge relationships is a fundamental cognitive characteristic and is the foundation for such learning phenomena as generalization and discrimination. However, relations may vary widely in their degree of abstraction (e.g., judging that two objects are identical versus judging the functional similarity of the phrases "dog is to dog house" and "bird is to nest"), and species may differ in their abilities to understand complex relationships (reviewed in Penn, Holyoak, & Povinelli, 2008).

A variety of laboratory studies have explored the dolphins' understanding of relationships (e.g., see summaries in Herman, 2006; Herman et al., 1994; Herman, Uyeyama, & Pack, 2008). One of the most fundamental relationships is the perceptual similarity between objects or sounds. The ability to judge "sameness" may be tested in the identity matching-to-sample (MTS) task and the same/different task. In the identity MTS task, a sample item is presented followed by several alternatives. The subjects' task is to identify the alternative that matches (i.e., is identical to) the sample. In the same/different task, the subject is presented with two sample items, either sequentially or simultaneously, and symbolically must indicate the relationship between the two (i.e., same or different). Through these tasks, dolphins have been shown capable of judging the similarity of two arbitrary sounds (e.g., Herman & Gordon, 1974; Thompson & Herman, 1977), two arbitrary objects (e.g., Herman, Hovancik, Gory, & Bradshaw, 1989; Mercado, Killebrew, Pack, Macha, & Herman, 2000), and the visual image of an object and its echoic counterpart (e.g., Herman et al., 1998; Pack & Herman, 1995). That the dolphins in these studies were able to match pairs of items on their first exposure provided strong evidence that they had acquired a "concept" of sameness (summarized in Herman et al., 1994). Furthermore, the dolphins acquired the matching concept relatively rapidly with limited set of exemplars (*cf.* Wright et al., 1988 for much lengthier training with pigeons). For one dolphin, the acquisition of the matching concept appeared immediate (Herman, Pack, et al., 1993). Although impressive, these types of judgments of relations are considered by Penn et al. (2008) to be of lower order because they are based on perceptual physical similarity.

At a more complex level (although still based on judgments of physical similarity), dolphins have been shown to understand the relationship between external stimuli and themselves. For example, bottlenose dolphins are one of the few species that can imitate both arbitrary sounds and motor behaviors (e.g., Richards, Wolz, & Herman, 1984; Xitco, 1988). In a review, Herman (2002) showed that dolphins are capable of the following forms of imitation: a) copying arbitrary synthetic sounds including spontaneous production of replicas across octaves, b) replicating their own previously performed motor behaviors, c) copying motor behaviors performed by another dolphin, and d) copying motor behaviors performed by a human, either "live" or displayed on a television monitor. Notice that because humans and dolphins do not possess identical body parts, to create an accurate facsimile in some instances, a dolphin must judge the relationship between a human's body parts and its own corresponding body parts through analogy (e.g., the human's arms and hands are analogous to the dolphin's pectoral fins, and the human's legs and feet are analogous to the dolphin's its tail flukes). Also, of relevance to the issue of the dolphin understanding the relations between external stimuli and themselves is a study by Reiss and Marino (2001) who showed that dolphins recognize the relationship between themselves and their image in a mirror. Mirror-self recognition has been shown in only a few species including humans, apes, dolphins and elephants (see review in Plotnik, de Waal, & Reiss, 2006).

Judgments of the relative relationships between stimuli. Ralston and Herman (1995) tested a dolphin's ability to discriminate various four-tone ascending-frequency stimuli from four-tone descending-frequency stimuli in which individual frequencies were represented in both ascending and descending sequences (i.e., ascending-frequency stimuli and descending-frequency stimuli had overlapping tones). The dolphin's above-chance performance levels in categorizing different sequences of tones as either ascending in frequency or descending in frequency demonstrated that it was able to judge the relative relationships between consecutive tones in a sequence rather than simply judging whether individual tones were either the same or different in frequency.

Judgments of the relations between concepts. Herman, Richards and Wolz (1984) trained two dolphins to respond to instructions given through sequences of symbols (gestures or sounds), in which each unique symbol referred to either a location modifier "L" (e.g., right and left), or an object of two different categories "T" = transportable, "S" = stationary (i.e., non-transportable), or a direct action "A" (i.e., performed directly to an object), or a relational action "R" requiring the creation of a relationship between two objects (e.g., putting one object next to another object, or putting one object atop another object). Using these object symbols, the dolphins were taught several grammatical sequences. Here, I focus only on the dolphin instructed through gestures. Herman et al. (1984) taught this dolphin the following grammatical frames using a subset of the total available symbols: "L + (T or S) + A" = perform the designated action "A" to the designated object "T or S" at the specified location "L", and "(T1 or S1) + T2 + R" = locate the second designated object "T2" and use it to create the specified relationship "R" with the first designated object "(T1 or S1)." For example, if given the sequence of three gestures "Right + Water (stream of water from a hose attached to the side of the pool) + Tail-touch" (an example of an L + S + A sequence), the dolphin located the stream of water to its right (ignoring the one to its left) and touched it with its tail flukes. If given the sequence "Surfboard + Hoop + In" (an example of a T1 + T2 + R sequence), the dolphin located the hoop, transported it to the surfboard and placed it on top of the surfboard. Following the training of the two frames with a limited set of exemplars, the dolphin spontaneously (on the first trial) was able to carry out instructions within these frames using objects not used within the training set. Of relevance to the issue of the dolphin's understanding of higher-order relations, it spontaneously (i.e., without any training) understood all of the following novel frames: (T1 or S1) + L (left or right) + T2 + R; L (left or right) + (T1 or S1) +T2 + R; and L (left or right) + (T1 or S1) + L (left or right) + T2 (Herman, 1986; Herman et al., 1984). Note that the meaning of any particular sequence is directly related to both the specific symbols used and the specific sequence of these symbols. That the dolphin carried out a multitude of novel instructions in these frames with high accuracy (see Herman, 1986) revealed that it took account of both the sequential-order rules (the syntactic component) and the referents of individual symbols (the semantic component). As pointed out by Herman et al. (2008), these responses provided evidence that the dolphin was able to infer a higher-order relation that resulted from the conjoining of first-order relations. It is important to note that in order to carry out these sequences with accuracy, the dolphin must be able to understand that how it responds to any object element within the sequence varies depending on the position of that object element in the sequence as well as the other elements present. For example, when the dolphin experiences a "T" element at the beginning of a sequence such as the gestural symbol for "Ball," it does not yet know if it will be required to act on that object directly (as in Ball + Toss = "go to the ball and toss it"), or indirectly by transporting another object to the Ball (as in Ball + Person + Fetch = "find the person and place him/her next to the ball"). Thus, accurate processing of symbolic sequences within the artificial language requires that the dolphin be cognitively flexible in its understanding of how symbols may function.

Herman, Kuczaj et al. (1993) revealed further examples of this cognitive flexibility when they presented the dolphin educated in the gestural language with "anomalous" sequences (i.e., novel sequences that violated the familiar syntactic structure or semantic rules of the original imposed language, Herman et al., 1984). Syntactic violations involved extended strings of symbols that violated the familiar syntactic structure of the language (e.g., S1 + S2 + T + R). In such cases, the dolphin spontaneously extracted subsets of elements that comprised a "legitimate" grammatical rule. For example, when given Speaker + Water + Pipe + In (an example of a syntactic violation), the dolphin tossed the pipe on top of the speaker, i.e., she ignored the second element, "Water" – see earlier definition, and combined non-adjacent elements to perform the subset Speaker + Pipe + In (Herman et al., 1993b). These types of extractions of subsets of elements were common. For example, in response to 19 anomalous four-element sequences of the types S + S + T + R, S + T + S + R, or S + T + T + R, the dolphin extracted a legitimate subset solely from the elements within the sequence on 12 occasions, 10 of which involved conjoining non-adjacent elements (Herman Kuczaj, et al., 1993). Semantic violations involved proper grammatical strings that violated a semantic rule for example, S1 + S2 + R which instructs the dolphin to transport a non-transportable object. In such instances, the dolphin rejected the instruction, either offering no response at all or sometimes substituting a transportable object for the specified non-transportable (Herman, Kuczaj et al., 1993). Notice that in order to construct and carry out meaningful responses to anomalous sequences that contain syntactic and semantic violations, the dolphin must understand the functional relationship of different grammatical frames to each other, the functional relationship of elemental positions within these grammatical frames, and the functional relationship of different categories of elements (i.e., which objects can be substituted as legitimate objects to be transported and which ones are non-transportable).

Evidence from the wild

As noted earlier, generalization and discrimination rely on judgments of similarity and difference. An animal's ability to understand relationships and to learn when to generalize and when to discriminate can significantly impact its survival and reproductive success. The reviewed laboratory evidence indicates that dolphins can understand relationships on the basis of both form and function. Field studies have revealed how these abilities manifest themselves in the wild in dolphin societies. In Sarasota Bay, Florida and Shark Bay, Western Australia pairs and trios of male bottlenose dolphins form relatively stable alliances that may persist for decades (reviewed in Connor, Wells, Mann, & Read, 2000). A function of these alliances (termed "first-order" alliances) is to secure females. In Shark Bay, first-order male alliances cooperate to isolate and consort single females (Connor, Richards, & Smolker, 1996; Connor, Smolker, & Richards, 1992a, b). Also, stable first-order male alliances may form second-order male alliances with one or two other first-order male alliances. Second order male alliances cooperate to "steal" the female consort from other male alliances and to defend against such attacks (Connor et al., 1992b). Connor, Heithaus and Barre (1999) have also described a "super-alliance" (an alliance consisting of 14 males in which individual males also maintain both the first-order and second-order levels required for stable alliances). Connor and Mann (2006) note several important aspects of the hierarchy of first- and second-order alliances that bear on the issue of the dolphin's understanding of relationships. First, relationships between individuals as well as between alliances are triadic and mediated by affiliative interactions. That is, through affiliative interactions, individual A may form an alliance with individual B against individual C. At a higher level, through affiliative interactions *alliance* A may form a second-order alliance with alliance B against alliance C. Thus, Shark Bay dolphins are linked as a community by a complex network of individual and group social relationships that are nested within one another. For male dolphins in Shark Bay, several cognitive challenges are immediately suggested that address the issue of understanding relationships. First, a male whose first-order alliance normally competes for females with other male first-order alliances must balance its competitive behavior with other affiliative behaviors to maintain bonds allowing second-order alliances to form. A second cognitive challenge is that this male must be able to form long-term memories of its own social relationships as well as those of other males within the social network. Finally, the male's mental representations of the social network of other dolphins must be labile (i.e., able to undergo frequent change) in order to accommodate any changes in its own social relationships and those of others with whom it interacts. Laboratory studies (see earlier section) have demonstrated cognitive abilities in judging relations that appear to support these speculations.

Synthesis

When taken together, the findings from the wild and the laboratory indicate that the dolphin has the ability to understand, interpret and reinterpret complex relationships including hierarchical relationships in its world. To process these relationships the dolphin can tap into broad concepts of similarity and difference that span modalities, possibly allowing them to form analogies (e.g., a wave of the trainer's foot outside the pool or on television is analogous to a wave of the dolphin's tail flukes). Such behavior requires considerable cognitive skill and flexibility. Connor and colleagues have suggested a cognitive system that enables male dolphins in Shark Bay to create mental representations that model their social network and levels of relationships (e.g., Connor & Mann, 2006). Such a model must be dynamic in that it must allow mental "weights" associated with the strength of specific relationships to be adjusted as a function of affiliative and agonistic interactions between males. Laboratory studies of the dolphin's responses to novel complex symbolic sequences, as well as syntactic and semantic anomalies that indicate an understanding of nested relationships and changing relationships between elements appear to access some of the same types of higher order relationship processing required for the types of interactions seen in Shark Bay. However, a cognitive model that can explain the type of frequently shifting alliance partnerships in the male super-alliance has yet to be developed. Males belonging to the super-alliance will form pairs and sometimes trios that consort females. At a second level, teams of first level trios will form and cooperate to attack other alliances. However, at each level the composition of a trio is flexible and may change between consortships (Connor et al., 1999). As pointed out by Connor and Krutzen (2003), a simple 'equivalence rule' (see Schusterman, Reichmuth, Kastak, & Kastak, 2003), such as individual males being classified as members of the super-alliance or not, and all members being treated the same, cannot explain the frequently shifting alliance partnerships within the super-alliance, because males within the super-alliance have preferences of certain males as alliance partners over others (Connor et al., 1999). Thus, the nested and varying relationships within the super-alliance suggest an understanding of higher-order relationships and equivalencies that require further verification in the laboratory.

Dolphin Understanding of Referential Symbolic Communication

Evidence from the laboratory

Referential symbolic communication is a sophisticated and complex form of communication involving social interactions that require the management of shared attention, and the use of symbols to refer to or point to something (Bates, 1976; Bruner, 1983). Savage-Rumbaugh (1986) suggests four components that are part of every referential communicative exchange. These are a) an arbitrary symbol that stands for and can act as a surrogate for something; b) a mental representation of the particular item related to the symbol such that when the symbol is produced it evokes the mental representation of the referenced item; c) an informant's intentional use of a symbol to communicate the stored knowledge in its mental representation about the item to another individual; and d) the recipient's appropriate decoding and responding to the informant's symbols. However as noted by Herman, Pack et al. (1993), referential competence may appear in different contexts, forms, and levels of development.

***Dolphin comprehension and production of symbolic references in artificial languages*.** Herman et al. (1984) taught two dolphins either that different human-initiated hand and arm gestures or computer-generated sounds were associated with different objects, agents, actions, and relationships. The dolphins were highly accurate in responding to imperative "sentences" by carrying out actions to named objects and creating relationships between named objects specified within symbolic sequences (e.g., see earlier rules associated with the dolphin taught to respond to human gestures). In a follow-up study, Herman and Forestell (1985) used the dolphin trained to respond to human language gestures to investigate its ability to respond to a trainer's interrogatives on the presence or absence of named objects in the dolphin's habitat. In response to a trainer signing an object symbol followed by a "question" gesture, the dolphin pressed either a paddle to its right (if the named object was present in its habitat) or a paddle to its left (if that object was absent). After learning to respond appropriately to these paddles using a small set of named objects, the dolphin spontaneously responded accurately when novel queries were made about named objects (i.e., those not used in training). The dolphin was as accurate at reporting object absence as object presence (Herman & Forestell, 1985). Inasmuch as the dolphin was spontaneously accurate in responding to novel queries about absent objects, the findings imply that object symbols and their referents were represented mentally such that when the symbol was produced it evoked the mental representation of the referenced item.

Herman, Pack et al. (1993) summarized the multiple uses and semantic functions of the object symbols taught by Herman et al. (1984) and from this provided a compelling argument that these symbols were understood as having a referring function. For example, the dolphin taught the gestural language understood that the symbol "Person" imbedded in the following different sequences "Person + Over," "Person + Surfboard + Fetch," "Surfboard + Person + Fetch," "Person Question," and "Person + Imitate" required the following responses respectively: a) to leap over the person and not any other object; b) to locate the surfboard and bring it to the person; c) to locate the person and bring him/her to the surfboard; d) to press one of two paddles depending on whether the person was present or absent; e) to copy the person's behavior, not the behavior of the other dolphin. Notice, that in some cases the object "Person" is to be responded to directly (e.g., leap over the person, or bring the person to the surfboard), in other cases indirectly (e.g., bring the surfboard to the person), and still in other cases not at all (i.e., report on whether the person is present or not, or observe the person's behavior and copy it). Such flexibility strongly supports the hypothesis that the dolphin understood the symbol "Person" referentially.

Two other laboratory studies of dolphin communication (Reiss & McCowan, 1993; Xitco, Gory, & Kuczaj, 2001) used underwater keyboards to investigate the dolphins' spontaneous use of keys in communicative exchanges with humans. Both keyboards were equipped with physical symbols representing items (e.g., objects, events, locations). Each symbol when activated also resulted in a unique acoustic associate being played underwater by a computer. The two dolphins in the Xitco et al. (2001) study appeared to understand the items associated with the symbols inasmuch as when symbols were activated by a human companion, the dolphin reportedly swam ahead of the human to the appropriate item and pointed to it while gazing back at the human (see below). Dolphins also spontaneously activated the keys. However, Xitco et al. (2001) provided no details on the validity of the dolphin's productions as demonstrating referential competence. In Reiss and McCowan (1993), two of four dolphins activated keys on a keyboard. They also spontaneously produced both imitations of symbol-associated sounds and productive facsimiles of sounds in conjunction with their associated objects or actions. However, data on symbol production was insufficient to consider the communication referential (as opposed to more basic associative learning).

Dolphin comprehension and production of symbolic references in natural vocal communication. Caldwell and Caldwell (1965) discovered that captive bottlenose dolphins produce individually distinctive pure tone whistles. They termed these "signature whistles" and they hypothesized that signature whistles functioned to publicize a dolphin's individual identity. A major effort was launched over the following four decades to examine how dolphins develop and use their signature whistles, the extent of their abilities to vocally learn another's signature whistle, and their ability to imitate sounds beyond signature whistles. A key question was whether signature whistles were used in symbolic referential communicative exchanges. Tyack (2003) reviews the history of laboratory and field studies of signature whistles and provides an excellent synthesis of the two. Laboratory studies have revealed the following: a) dolphins can imitate arbitrary non-natural sounds and can produce these sounds to label objects that have been previously associated with these sounds (Reiss & McCowan, 1993; Richards et al., 1984); b) dolphins do not inherit their signature whistles from their parents but rather develop their signature whistles by learning to imitate particular sounds present in their natal habitat (reviewed in Tyack & Sayigh, 1997); c) signature whistles of adult females are more stable over time than signature whistles of males, some of whom vocally converge on similar whistles with close male associates (Caldwell, Caldwell & Tyack, 1990); d) dolphins learn to imitate the signature whistles of other dolphins with whom they interact (Tyack, 1986); and e) an individual dolphin is more likely to produce its own signature whistle when isolated from a familiar group of dolphins than when the group remains cohesive (Janik & Slater, 1998). This latter finding suggested to Janik and Slater (1998) that signature whistles may function as contact calls between adults.

Evidence from the wild

No studies of referential symbolic communication using artificial language systems with wild dolphins have been published. However, a variety of field studies have examined dolphin use of signature whistles. Some of these studies have provided external validity for earlier findings using laboratory dolphins (see Tyack, 2003) while others have extended the current understanding of these vocalizations. For example, beyond the general finding from the laboratory that the signature whistles developed by young dolphins tend to be different from their mothers (e.g., Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997). Sayigh, Tyack, Wells, Scott and Irvine (1995) showed that male offspring are more likely than female offspring to produce signature whistles similar to their mothers, a finding that seems to fit well with the association patterns of maturing male and female bottlenose dolphins (see Connor et al., 2000).

With regard to the issue of referential communication, Sayigh et al. (1999) provided evidence that mothers responded preferentially to playbacks of their offspring's signature whistles and vice versa. Thus, dolphins appear to recognize the signature whistles of close associates. A second feature of symbolic referential communication is that symbols are learned. Smolker and Pepper (1999) provided evidence that three male dolphins upon forming a male-male coalition adopted (converged on) the same predominant whistle over a two-year period. Watwood, Tyack and Wells (2004) showed that this type of convergence of whistles by males is not simply a function of males experiencing a similar acoustic environment at an early age and creating similar whistles based on this shared experience. For example, although strongly bonded partners from the same subadult social group developed similar whistles, other males from that same subadult social group did not develop similar whistles (Watwood et al., 2004). These findings lead Watwood et al. to suggest that vocal learning was responsible for whistle sharing among male dolphins, a finding that finds support from earlier reviewed laboratory studies showing that dolphins readily imitate the signature whistles of close associates (e.g., Tyack, 1986) and can readily learn to imitate arbitrary synthetic sounds (Reiss & McCowan, 1993; Richards et al., 1984).

Finally, is there any evidence that dolphins use learned signature whistles in the wild to contact other dolphins? Using a hydrophone array to determine the location of vocalizing dolphins, Janik (2000) showed that wild dolphins often spontaneously match the whistle of another dolphin that is within acoustic range but out of visual range. Janik (2000) suggested that these dolphins were addressing each other through these closely coordinated vocal exchanges of learned whistles.

Synthesis

Thus far, findings on dolphin communication (either through artificial symbolic systems or natural vocal systems) appear to fulfill some of the criteria set forth by Savage-Rumbaugh (1986) for referential communicative exchange. Compelling evidence exists in the domain of receptive competencies (see Herman & Morrel-Samuels, 1990 for a discussion of asymmetries in receptive and productive language competency). Laboratory studies have shown that the dolphin can understand that a symbol can stand for something, can form a mental representation of the item related to the symbol, and can appropriately decode and respond to a human trainer's symbols (summarized in Herman, Pack et al., 1993). The fourth requisite, a dolphin's intentional use of a symbol to communicate the stored knowledge about an item to another individual has yet to be substantiated beyond the studies of Herman and Forestell (1985, see above) that showed that a dolphin could use paddles that symbolically are associated with "presence" and "absence" to report its stored knowledge on the presence or absence of objects in its habitat. Follow-up studies to those initiated by Reiss and McCowan (1993) and Xitco et al. (2001) in which dolphins are provided with tools to both comprehend and produce symbolic communications should be carried out.

With respect to a dolphin's natural vocal communications, both laboratory and field studies have added significantly to our understanding of the degree of referential quality of dolphin vocalizations. Thus far only the signature whistle has been shown to possess some features of a referential symbol. However, although Janik's (2000) study is consistent with the idea of signature whistles as learned symbols used in referential exchanges, it is unknown to what extent these whistles evoke mental representations of individual dolphins. Tyack (2003) suggests that a cross-modal matching-to-sample type of laboratory study that examines if a dolphin listening to a signature whistle of another can select the visual representation of that same individual might provide such evidence. However, recognition from whistle to visual image would have to be spontaneous (i.e., on the first trial) as anything beyond this would be subject to interpretations based on associative learning between sights and sounds (see Pack et al., 2004). As described earlier, spontaneous cross-modal matching of arbitrary objects across the senses of vision and echolocation has been demonstrated previously in laboratory studies (e.g., Herman et al., 1998; Pack & Herman, 1995) and may provide a foundation for dolphins to match an individual's signature whistle spontaneously to its visual image. Finally, in addition to signature whistles, more attention should be given to the investigation of other dolphin sounds such as burst pulse sounds and their possible referential qualities (e.g., Herzing, 1996).

Dolphin Understanding of the Management of Joint Attention

Evidence from the laboratory

As noted earlier, an important component of symbolic referential communication is the management of shared attention. Shared or *joint attention* refers to the triadic transaction between an informant, a receiver, and an object, an event, or a place of interest (see Pack & Herman, 2006 for a review). Joint attention is an important component of social cognition that can benefit the receiver, the informant, or both. For example, joint attention can provide the receiver with enhanced perceptual alertness to items of biological or social significance (e.g., predators, prey, mates, rivals, etc.). Not only may the receiver learn where or at what the informant is attending, but may also gain knowledge about the beliefs or desires of the informant that may be exploited to benefit the receiver. Conversely, by directing the receiver's attention, the informant can benefit by manipulating the receiver's behavior (e.g., by receiving assistance with monitoring, obtaining, or defending against the focal subject of the informant's point or gaze). Thus, an ability to manage joint attention has the potential to have significant value for social individuals.

Joint attention has often been investigated in the laboratory by examining an individual's understanding and use of pointing and gazing cues. Several laboratory studies have investigated the dolphins' understanding of human directed pointing and gazing including whether these signals are understood referentially. These studies were summarized by Pack and Herman (2006) and showed that: a) test naïve dolphins responded accurately on first trials to human-initiated *dynamic* pointing cues directed at objects placed to the right and left (Tschudin, Call, Dunbar, Harris, & van der Elst, 2001); b) test sophisticated dolphins responded accurately on first trials to human-initiated dynamic pointing cues directed at distal objects including objects placed behind the dolphin (Herman et al., 1999); c) test sophisticated dolphins responded accurately on first trials when human-initiated points were substituted for objects symbols within familiar sequences of symbols instructing the dolphin to create relationships between symbolically referenced objects (Herman et al., 1999; Herman & Uyeyama, 1999); d) test sophisticated dolphins responded accurately on first trials to human-initiated dynamic gazing cues, static gazing cues and static pointing cues directed at objects, and could ignore non-indicated objects in the path of directed points (Pack & Herman, 2004, 2007); and e) test sophisticated dolphins could form mental representations of objects pointed to or gazed at that required remembering those objects (Herman et al., 1999; Pack & Herman, 2007).

Other studies have examined the spontaneous development of pointing behavior in the dolphin and whether this behavior is contingent on the attention of a receiver (Xitco et al., 2001; Xitco, Gory, & Kuczaj, 2004). Xitco et al. (2001) exposed two dolphins to human divers using an underwater keyboard that contained symbols representing goal objects (e.g., foods, toys, tools) or locations within the habitat. Divers modeled the functional use of these keys in the presence of the dolphins (i.e., without training the dolphins). After approximately 6 months, each dolphin, in the presence of a diver, began spontaneously “pointing” at goal objects housed within containers (which they could not access without a human’s assistance) by adopting a stationary position in front of a container and aligning the rostrum and the longitudinal axis of the body with the goal object. Importantly, while pointing, the dolphin often engaged in monitoring of a human diving companion by turning its head sideways towards the diver while maintaining its body alignment to the object. This type of monitoring is a key component of joint attention as well as the production of referential communication through pointing (Pack & Herman, 2006). The diver’s response to the dolphin’s behavior was to open the container and provide the goal object housed inside.

Xitco et al. (2001) reported the following characteristics of pointing events: a) pointing by dolphins only occurred when human diving companions were present (an indicator that the dolphin’s pointing behavior was intended to direct the diver); b) monitoring was more likely to accompany pointing when the dolphin pointed to relatively distant objects and when divers were far from the pointing dolphin; c) dolphins were more likely to refrain from pointing when divers were nearby. In a follow-up study, Xitco et al. (2004) found that the dolphin’s pointing behavior was conditional upon the attentiveness of the human receiver. For example, little pointing occurred when the receiver had his back turned or swam away compared to when the receiver was face-forward (i.e., in an advantageous position for observing the dolphin’s pointing behavior).

Evidence from the wild

Dolphin cooperative behaviors in the wild may be considered to involve joint attention inasmuch as they involve two or more individuals working together and taking into account each other’s actions to exploit an object of interest (see Perelberg & Schuster, 2008 for a review). For example, several studies have documented cooperative foraging in bottlenose and other dolphin species (e.g., Benoit-Bird & Au, 2009; Connor et al., 2000; Reynolds, Wells, & Eide, 2000), cooperative inter-and intraspecific aggression (e.g., Herzing & Johnson, 1997), and cooperative mate coercion and mate stealing by male partners and alliances (see summaries in Connor et al., 2000; Connor & Mann, 2006).

With respect to directed cuing (e.g., pointing) as a form of managed joint attention, there has been little systematic study in dolphins in the wild. However recently, Bender et al. (2008) provided some of the most compelling evidence for joint attention as it relates social learning and teaching of foraging tactics between mothers and their calves in Atlantic spotted dolphins. Bender et al. (2008) analyzed videotapes of underwater foraging behavior of mothers in three different contexts: in the presence of their calves, when they were alone, and when they were with another non-calf dolphin. They found that mothers pursued prey longer and made more referential body-orienting movements in the direction of the prey while foraging when their calves were present than when their calves were absent, regardless of whether they were alone or another non-calf dolphin was present

(Bender et al., 2008). Importantly, rather than immediately grabbing and eating prey in the presence of their calves, mothers manipulated prey over a protracted period while their calves observed. Furthermore, in some instances, a mother allowed its calf to ingest the prey even though the calf was still nursing and not dependent on the prey for sustenance (Bender et al., 2008). That calves ultimately benefited from their mother's models may be seen from the dolphins who, as adults, employed the same teaching tactics with their own calves that they experienced previously from their mothers. Aside from fulfilling some of the principal requirements for true pedagogy as described by Caro and Hauser (1992), this study shows the triadic transaction characteristics of joint attention, specifically the informant (mother) directing the attention of a recipient (its calf) through body orientation (i.e., pointing, see Xitco et al., 2001) towards an object (in this case, prey) of interest. For pointing to be considered referential, it should be coordinated closely with the receiver's attentional state (Tomasello, 1995), which in many instances may be inferred from the receiver's face or body orientation (e.g., head facing the target object of the informant). Bender et al. (2008) provide evidence that while present during their mother's foraging events, calves were positioned advantageously for close observation of their mother's prey chases.

Synthesis

Cooperation appears to be a key element in many areas of bottlenose dolphin society as well as in the societies of several other delphinid species (e.g., Connor et al., 2000; Herzing & Johnson, 1997). Whether the object of attention is a food resource, an enemy, or a potential mate, for coordinated behaviors to be maximally effective, individuals must ensure that their collaborators are attentive. Laboratory studies have provided strong evidence that management of joint attention in dolphins is well developed and symmetric in terms of receptive and productive competencies (Herman et al., 1999; Pack & Herman, 2004, 2007; Xitco et al., 2001, 2004). They have demonstrated that dolphins understand the referring function of a human's directed pointing and gazing cues, and can exploit this knowledge to actively direct a human's behavior (summarized in Pack & Herman, 2006). The dolphins' demonstrated "pointing" skills in the laboratory appear to indicate a mastery of the proto-declarative as described by Bates (1976) for the advanced pointing behavior of pre-verbal human infants. This type of directed pointing skill has been demonstrated in at least one study in the wild involving mothers teaching their calves foraging techniques (Bender et al., 2008). Future field studies should examine for the active management of joint attention in other cooperative activities between dolphins (Perelberg & Schuster, 2008). Future laboratory studies should continue to investigate the mechanisms underlying managed joint attention skills as well as the extent to which dolphins engaged in joint attention are cognizant of not only each other's shared attention toward an item of interest but also each other's shared state of knowledge regarding that item (e.g., Call & Tomasello, 1999; Premack & Woodruff, 1978).

Conclusions

I began this paper with the premise that, as in other fields of animal behavior, there is a synergistic relationship between laboratory studies and field studies of dolphin behavior and cognition. The foundation for this premise is that: a) laboratory studies of dolphin behavior can provide certain types of information on dolphin cognition that cannot be obtained in the field; b) field studies of dolphin behavior can provide certain types of information on dolphin cognition that cannot be obtained in the laboratory; c) findings from laboratory studies of dolphin behavior and cognition can contribute information and ideas to field studies and vice versa; d) neither laboratory studies alone nor field studies alone can fully describe dolphin cognition; and e) it is the integration of findings from the laboratory and field that provides the most complete and compelling case for understanding dolphin cognition, and importantly that provides external validity for many observations in the laboratory. The synergistic relationship between laboratory studies and field studies of dolphin behavior and cognition and the benefit of the synthesis of data from both areas towards a greater understanding of dolphin cognition was demonstrated through examples in four areas of dolphin cognition. In each case, the combined data from laboratory and field provided a more complete explanation of the area under study than did either one alone. Furthermore, in many cases information derived from the laboratory positively influenced the development of studies and the interpretation of studies in the field and vice versa. Thus, the combined effect of both areas was greater than simply the sum of their individual effects. This implies that future attempts to describe aspects of dolphin behavior and cognition would greatly benefit from both laboratory and field studies.

Figure 1 presents a visual representation of a synergistic approach for understanding dolphin behavior and cognition from laboratory and field studies. At the base, individual nodes represent the data, findings, and theories derived separately from laboratory studies and field studies. Each node includes a large non-overlapping portion that reflects the unique contributions that can be made from laboratory and field studies (see Table 1). The overlap between the base nodes largely reflects the ability to use similar methods in the laboratory and in the field (e.g., recording behaviors or sounds from individuals). However, in some cases this may yield different results and/or different interpretations of results reflecting the differences between laboratory and natural settings (e.g., the employment and function of “signature whistles” by dolphins, summarized in Tyack, 2003). The bi-directional arrow between the base nodes reflects the sharing of information between laboratory and field studies and the influence each has on the other to inspire, shape, and modify questions and approaches. The second level shows a single node representing overarching theories that emerge from the accumulation of data within each base node and synthesis of data across the base nodes. Bi-directional arrows indicate the influence of any theory on future research directions in the laboratory and field. Finally, all three nodes are housed within an evolutionary and comparative framework (see Tyack, 1993, for a similar perspective). Cognitive characteristics are subject to the same evolutionary pressures as other behavioral traits. Therefore, it is important to consider what types of pressures (e.g., environmental, social) may have lead to the types of sensory, cognitive, and communicative capabilities and specializations that are being revealed in dolphins and how these relate to similar abilities and specializations observed in other species (e.g., the extent to which we see cognitive convergence with other distantly related species subject to similar pressures) (e.g., Connor, 2007; Reiss & Marino, 2001).

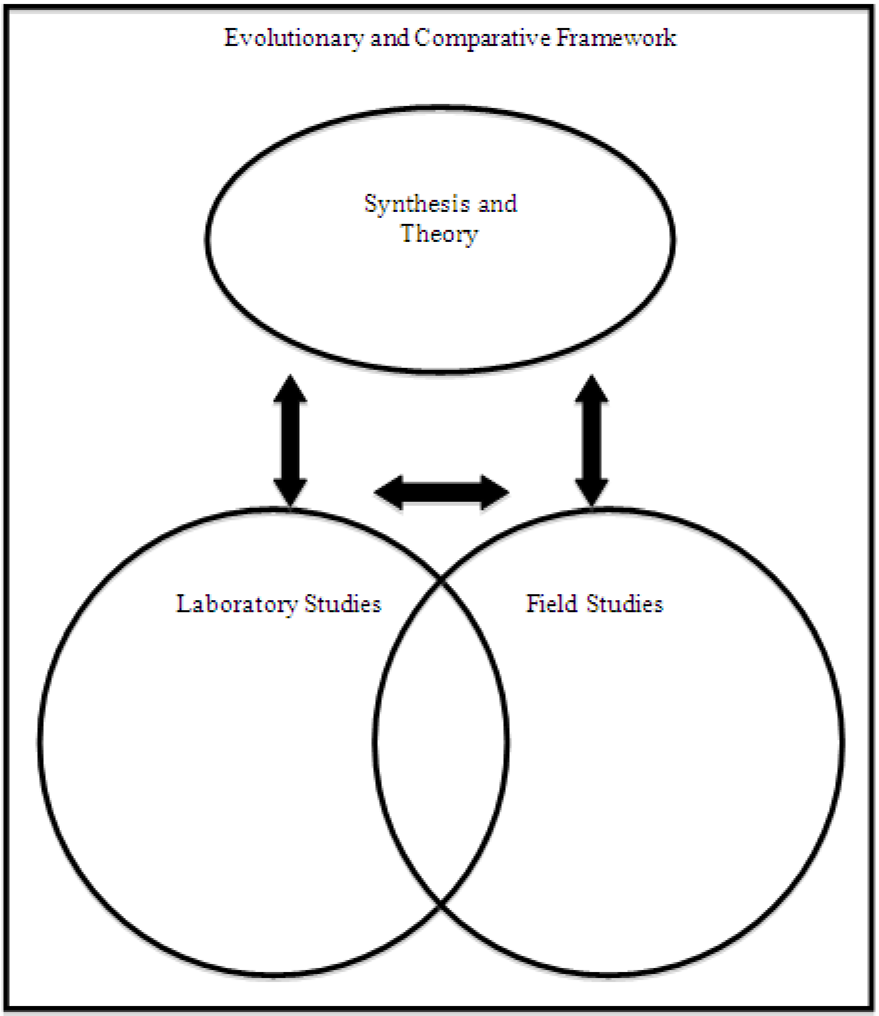

Figure 1. Theoretical approach to the study of dolphin behavior and cognition that incorporates the synergistic relationship between laboratory and field studies.

References

Au, W. W. L. (1993). *The sonar of dolphins*. New York: Springer-Verlag.

Au, W. W. L., & Herzing, D. L. (2003). Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*). *Journal of the Acoustical Society of America, 113*, 598-604.

Au, W. W. L., Schusterman, R. J., & Kersting, D. A. (1980). Sphere-cylinder discrimination via echolocation by *Tursiops truncatus*. In R.-G. Busnel & J. F. Fish (Eds.), *Animal sonar systems* (pp. 859-862). New York: Plenum Press.

Balda, R. P, Pepperberg, I. M., & Kamil, A. C. (1998). *Animal cognition in nature: The convergence of psychology and biology in laboratory and field*. New York: Academic Press.

Barta, R. E. (1969). Acoustic pattern discrimination by an Atlantic bottle-nosed dolphin. Unpublished manuscript. Naval Undersea Center, San Diego, CA.

Bates, E. (1976). *Language and context: The acquisition of pragmatics*. New York: Academic Press.

Bender, C. E., Herzing, D. L, & Bjorklund, D. F. (2008). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition*, *12*, 43-53.

Benoit-Bird, K. J., & Au, W. W. L (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *Journal of the Acoustical Society of America*, *125*, 125-137.

British Broadcasting Company (2003). Dolphins: Deep thinkers. *Wildlife on one series*. BBC Television.

Bruner, J. S. (1983). *Child's talk: Learning to use language*. New York: W. W. Norton.

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus). Science*, *207*, 434-435.

Caldwell, M. C., & Caldwell, D. K. (1979). The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*): Ontogeny. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals: Current perspectives in research. vol.3 cetaceans.* (pp. 369-401). New York: Plenum Press.

Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus*. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin: Recent progress in research* (pp. 199-234). San Diego, CA: Academic Press.

Call, J., & Tomasello, M. (1999). A nonverbal false belief task: The performance of children and great apes. *Child Development, 70,* 381-395.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology, 67,* 151-174.

Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species.* Chicago: University of Chicago Press.

Connor, R. C. (2007). Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 587-602.

Connor, R. C., Heithaus, R. M., & Barre, L. M. (1999). Super-alliance of bottlenose dolphins. *Nature*, *371*, 571-572.

Connor, R. S., & Krutzen, M. (2003). Levels and patterns in dolphin alliance formation. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence,* *culture and individualized societies* (pp. 115-120), Cambridge, MA: Harvard University Press.

Connor, R. C., & Mann, J. (2006). Social cognition in the wild: Machiavellian dolphins? In S. Hurley & M. Nudds (Eds.), *Rational animals?* (pp. 329-367). Oxford, UK: Oxford University Press.

Connor, R. C., Richards, A. F., Smolker, R. A., & Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*, *133*, 37-69.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992a). Dolphin alliances and coalitions. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415-443). New York: Oxford University Press.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992b). Two levels of alliance formation among bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences, 89*, 987-990.

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

de Waal, F. B. M., & Tyack, P. L. (2003). *Animal social complexity: Intelligence, culture, and individual societies*. Cambridge, MA: Harvard University Press.

Harley, H. E., Putman, E. A., & Roitblat, H. L. (2003). Bottlenose dolphins perceive object features through echolocation. *Nature, 424*, 667-669.

Herman, L. M. (1980). Cognitive characteristics of dolphins. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 363-421). New York: Wiley-Interscience.

Herman, L. M. (1986). Cognition and language competencies of bottlenosed dolphins. In R. J. Schusterman, J. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 221-251). Hillsdale, NJ: Lawrence Erlbaum Associates.

Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In C. Nehaniv & K Dautenhahn (Eds.), *Imitation in animals and artifacts.* (pp. 63-108). Cambridge, MA: MIT Press.

Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley & M. Nudds (Eds.), *Rational animals?* (pp. 439-467). Oxford, UK: Oxford University Press.

Herman, L. M., Abichandani, S. L., Elhajj, A. N., Herman, E. Y. K., Sanchez, J. L., & Pack, A. A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology, 113*, 1-18.

Herman, L. M., & Forestell, P. H. (1985). Reporting presence or absence of named objects by a language-trained dolphin. *Neuroscience and Biobehavioral Reviews, 9, 667-691*.

Herman, L. M., & Gordon, J. A. (1974). Auditory delayed matching in the bottlenosed dolphin. *Journal of the Experimental Analysis of Behavior, 21*, 19-26.

Herman, L. M., Hovancik, J. R., Gory, J. D., & Bradshaw, G. L. (1989). Generalization of visual matching by a bottlenosed dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual or auditory materials. *Journal of Experimental Psychology: Animal Behavior Processes, 15*, 124-136.

Herman, L. M., Kuczaj, S. A., II, & Holder, M. D. (1993). Responses to anomalous gestural sequences by a language-trained dolphin: Evidence for processing of semantic and syntactic information: *Journal of Experimental Psychology: General*, *122*, 184-194.

Herman, L. M., & Morrel-Samuels, P. (1990). Knowledge acquisition and asymmetries between language comprehension and production: Dolphins and apes as a general model for animals. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and explanation in the study of behavior: Vol. 1: Interpretation, intentionality, and communication*. (pp. 283-312). Boulder, CO: Westview Press.

Herman, L. M., & Pack, A. A. (1992). Echoic-visual cross-modal recognition by a dolphin. In J. R. Thomas, R. A. Kastelein, & A Ya. Supin (Eds.), *Sensory Processes of Marine Mammals*, (pp. 709-726). New York: Plenum.

Herman, L. M., Pack, A. A., & Hoffmann-Kuhnt, M. (1998). Seeing through sound: Dolphins perceive the spatial structure of objects through echolocation. *Journal of Comparative Psychology, 112,* 292-305.

Herman, L. M., Pack A. A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. R. Roitblat, L. M. Herman, & P. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 273-298). Hillsdale, NJ: Lawrence Erlbaum.

Herman, L. M., Pack, A. A., & Wood, A. M. (1994). Bottlenosed dolphins can generalize rules and develop abstract concepts. *Marine Mammal Science*, *10*, 70-80.

Herman, L. M., Richards, D. G., & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16,* 129-219.

Herman, L. M., & Uyeyama, R. K. (1999). The dolphin's grammatical competency: Comments on Kako (1998). *Animal Learning and Behavior, 27,* 18-23.

Herman, L. M., Uyeyama, R. K., & Pack, A. A. (2008). Bottlenose dolphins understand relationships between concepts. *Behavioral and Brain Sciences, 31,* 139-140.

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

Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: Implications for a sound society. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing in whales and dolphins* (pp. 225-272). New York: Springer-Verlag.

Herzing, D. L. (2004). Social and nonsocial used of echolocation in free-ranging *Stenella frontalis* and *Tursiops truncatus*. In J. Thomas, C. Moss, & M. Vater (Eds.), *Advances in the study of echolocation in bats and dolphins* (pp. 404-410). Chicago: University of Chicago Press.

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.

Highfill, L. E., & Kuczaj, S. A., II. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic Mammals, 33,* 380-389.

Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science, 289*, 1355-1357.

Janik, V. M., & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphins signature whistles are cohesion calls. *Animal Behaviour, 56,* 829-838.

Kellogg, W. N., & Kohler, R. (1952). Responses of the porpoise to ultrasonic frequencies. *Science*, *116*, 250-252.

Killebrew, D. A., Mercado, E. M., III, Herman, L. M., & Pack, A. A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals 21*, 34-44.

Kuczaj, S. A., II, Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. 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.

Lammers, M. O., & Castellote, M. (2009). The beluga whale produces two pulses to form its sonar signal. *Biology Letters, 5,* 297-301. doi:10.1098/rsbl.2008.0782

Marino, L., Connor, R. C., Ewan Fordyce, R., Herman, L. M., Hof, P. R., Lefebvre, L., et al. (2007). Cetaceans have complex brains for complex cognition. *PLoS Biology, 5*, 966-972.

McCowan, B., & Reiss, D. (1995a). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (*Delphinidae, Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. *Ethology*, *100*, 194-209.

McCowan, B., & Reiss, D. (1995b). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology, 109*, 242-260.

McCowan, B., & Reiss, D. (1995c). Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): Wide band, low frequency signals during mother/aunt-infant interactions. *Zoo Biology, 14,* 293-309.

McBride, A. F. (1956). Evidence for echolocation by cetaceans. *Deep-Sea Research, 3,* 153-154.

Mercado, E. M., III, Killebrew, D. A., Pack, A. A., Macha, I. V. B., & Herman, L. M. (2000). Generalization of same-different classification abilities in bottlenosed dolphins. *Behavioural Processes, 50,* 79-94.

Nachtigall, P. E., Mooney, T. A., Taylor, K. A., Miller, L. A., Rasmussen, M. H., Akamatsu, T., et al. (2008). Shipboard measurements of the hearing of the white-beaked dolphin *Lagenorhynchus albirostris*. *The Journal of Experimental Biology*, *211*, 642-647.

Nachtigall, P. E., Murchison, A. E., & Au, W. W. L. (1980). Cylinder and cube discrimination by an echolocating bottlenose dolphin. In R-G. Busnel & J. F. Fish (Eds.), *Animal sonar systems* (pp. 945-947). New York: Plenum Press.

Nachtigall, P. E., Supin, A. Y., Pawloski, J. L., & Au, W. W. L. (2004). Temporary threshold shifts after noise exposure in the bottlenose dolphin (*Tursiops truncatus*) measured using evoked auditory potentials. *Marine Mammal Science, 20,* 673-687.

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

Pack, A. A. & Herman, L. M. (1993, November) (symposium organizers). *The range of dolphin echolocation*. In Abstracts of the 19th Biennial Conference on the Biology of Marine Mammals (pp. 11-12). Galveston, Texas: Society for Marine Mammalogy.

Pack, A. A., & Herman L. M. (1995). Sensory integration in the bottlenosed dolphin: Immediate recognition of complex shapes across the senses of echolocation and vision. *Journal of the Acoustical Society of America*, *98*, 722-733.

Pack, A. A., & Herman, L. M. (2004). 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.

Pack, A. A., & Herman, L. M. (2006). Dolphin social cognition and joint attention: Our current understanding. *Aquatic Mammals, 32,* 443-460.

Pack, A. A., & Herman, L. M. (2007). The dolphin's (*Tursiops truncatus*) understanding of human gaze and pointing: Knowing *what* and *where*. *Journal of Comparative Psychology, 121,* 34-45.

Pack, A. A., Herman, L. M., & Hoffmann-Kuhnt, M. (2004). Dolphin echolocation shape perception: From sound to object. In J. Thomas, C. Moss, & M. Vater (Eds.), *Advances in the study of echolocation in bats and dolphins* (pp. 288-298). Chicago: University of Chicago Press.

Pack, A. A., Herman, L. M., Hoffmann-Kuhnt, M., & Branstetter, B. K. (2002). The object behind the echo: Dolphins (*Tursiops truncatus*) perceive object shape globally through echolocation. *Behavioural Processes, 58*, 1-26.

Penn, D. C., Holyoak, K. J., & Povinelli, D. J. (2008). Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences, 31*, 109-178.

Perelberg, A., & Schuster, R. (2008). Coordinated breathing in bottlenose dolphins (*Tursiops truncatus*) as cooperation: Integrating proximate and ultimate explanations. *Journal of Comparative Psychology, 122*, 109-120.

Perelberg, A., & Schuster, R. (2009). Bottlenose dolphins (*Tursiops truncatus*) prefer to cooperate when petted: Integrating proximate and ultimate explanations II. *Journal of Comparative Psychology, 123*, 45-55.

Plotnik, J. M., de Waal, F. B. M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences, 103*, 17053-17057.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 1*, 515-526.

Ralston, J. V., & Herman, L. M. (1995). Perception and generalization of frequency contours by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology, 109*, 268-277.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case for cognitive convergence. *Proceedings of the National Academy of Sciences, 89*, 5837-5942.

Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenosed dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology, 107*, 301-312.

Reynolds, J. E., Wells, R. S., & Eide, S. D. (2000). *The bottlenose dolphin: Biology and conservation*. Gainsville, FL: University Press of Florida.

Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology, 98*, 10-28.

Rose, N. A., Parsons, E. C. M., & Farinato, R. (2009). *The case against marine mammals in captivity, 4th edition*. The Humane Society of the United States and the World Society for the Protection of Animals.

Rossbach, K. A., & Herzing, D. L. (1997). Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Marine Mammal Science, 13*, 498-504.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol*. New York: Columbia University Press.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Scott, M. D., & Irvine, A. B. (1995). Sex difference in whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology, 36*, 171-177.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A., Scott, M. D., & Irvine, A. B. (1999). Individual recognition in wild bottlenose dolphins: A field test using playback experiments. *Animal Behaviour, 57*, 41-50.

Schusterman, R. J., Reichmuth Kastak, C., & Kastak, D. (2003). In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture and individualized societies* (pp. 179-206). Cambridge, MA: Harvard University Press.

Simmons, J. A. (1989). A view of the world through bat's ear: The formation of acoustic images in echolocation. *Cognition, 33,* 155-199.

Smolker, R. A., & Pepper, J. W. (1999). Whistle convergence among allied male bottlenose dolphins (*Delphinidae, Tursiops* sp.*). Ethology*, *105,* 595-617.

Thompson, R. K. R., & Herman, L. M. (1977). Memory for lists of sounds by the bottlenosed dolphin: Convergence of memory processes with humans? *Science, 195*, 501-503.

Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origin and role in development* (pp. 103-130). Hillsdale, NJ: Erlbaum.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford, UK: Oxford University Press.

Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology, 115*, 100-105.

Tyack, P. L. (1986). Whistle repertoires of two bottlenosed dolphins, Tursiops truncatus: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, *18,* 251-257.

Tyack, P. L. (1993). Animal language research needs a broader comparative and evolutionary framework. In H. R. Roitblat, L. M. Herman, & P. Nachtigall (Eds.). *Language and communication: Comparative perspectives* (pp. 115-152). Hillsdale, NJ: Lawrence Erlbaum.

Tyack, P. L. (2003). Dolphins communicate about individual-specific relationships. In F. B. M. de Waal and P. L. Tyack (Eds.). *Animal social complexity: Intelligence, culture and individualized societies* (pp. 342-361). Cambridge, MA: Harvard University Press.

Tyack, P. L., & Sayigh, L. S. (1997). Vocal leaning in cetaceans. In C. Snowdon & M. Hausberger (Eds.), *Social influence on vocal development* (pp. 208-233). Cambridge, MA: Cambridge University Press.

Watwood, S. L., Tyack, P. L., & Wells, R. S. (2004). Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, *55*, 531-543.

Xitco, M. J. (1988). *Mimicry of modeled behaviors by bottlenose dolphins.* Unpublished master's thesis, University of Hawaii, Honolulu.

Xitco, M. J., Gory, J. D., & Kuczaj, S. A., II. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition, 4*, 115-123.

Xitco, M. J., Gory, J. D., & Kuczaj, S. A., II. (2004). Dolphin pointing is linked to the attentional behavior of a receiver. *Animal Cognition, 7*, 231-238.

Xitco, M. J., & Roitblat, H. L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Animal Learning and Behavior, 24,* 355-365.