

# Cognitive Implications of Synchrony in Dolphins: A Review

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## Abstract

Synchronous behaviors by dolphins in the wild are noted repeatedly. Recent fine-tuned assessments in the laboratory of the development of synchrony in newborn calves vis-à-vis their mothers highlight the strong predisposition of mother-calf pairs to spend most of their time behaving synchronously. Because dolphin calves apparently move continuously for the first month of their lives and stop comparatively infrequently for the first three months, the substantial energetic benefit they gain through slipstreaming may provide a mandate for mother-calf synchrony in terms of calf survival. We speculate that this constant intimate contact may lead to a succession of developmental stages in the calf that proceed from passive to active maintenance of synchrony and ultimately to imitation. This progression may explain shared within-group behaviors like mud-bank fishing, sponging, and herding.

**Key Words:** cetacean, dolphin, synchrony, synchronous movement, imitation, development of behavior, applied cognition, observational learning

## Introduction

The facility at behavioral imitation demonstrated by bottlenose dolphins (*Tursiops truncatus*) (Xitco, 1988; Herman et al., 1993; Bauer & Johnson, 1994; Harley et al., 1998; Xitco et al., 1998; Bauer & Harley, 2001; Herman, 2002) suggests an important learning mechanism for cultural transmission in this species (Rendell & Whitehead, 2001). (For this manuscript, imitation is defined as learning an unfamiliar, nonspecies-specific behavior from observing a model, cf. Thorpe, 1963; Whiten & Ham, 1992; Zentall, 1998; and others.) Learning through imitation provides a rapid means of modifying existing behaviors and acquiring new ones. How this imitative ability develops is not yet known, but behavioral synchrony may be an important precursor in dolphins. We review some of the pertinent data on synchrony and imitation in dolphins and speculate on their relationship.

Synchronous movement by cetaceans has been described in a variety of contexts, including traveling (Bel'kovich, 1991); coordinated hunting maneuvers (Saayman et al., 1973); affiliative and aggressive social encounters (Saayman et al., 1973; Pryor & Shallenberger, 1991; Connor et al., 1992a, 1992b, 2000); infant care (Bel'kovich, 1991; Johnson & Norris, 1994); and possibly "instruction" (Johnson & Norris, 1994), which may take the form of apprenticeship as has been described for some primates (cf. Matsuzawa, 2003). Notably, infant bottlenose dolphins spend a high proportion of their time moving synchronously with caregivers during the dependency period (Miles & Herzing, 2003; Fellner et al., 2005). The term *synchrony* is often left undefined, but typically it includes animals in proximity to each other, performing the same behavior at the same time, usually in parallel orientation. Although many of the functions of synchrony in dolphins may be shared with other schooling or flocking species (see reviews in Norris & Schilt, 1988, and Norris & Johnson, 1994), we propose that synchrony may serve the additional role of promoting social learning via imitation in dolphins.

## *Common Functions of Synchronous Movement*

Flocking birds and schooling fish receive a modest aero- or hydrodynamic advantage by moving in polarized or synchronized groups over those that move in loose aggregations (Breder, 1965; Cutts & Speakman, 1994; Boyd & Parsons, 1998; Herskin & Steffensen, 1998). Dolphin calves are frequently observed riding the wake of their mothers' pressure waves—that is, slipstreaming (Norris & Prescott, 1961)—through which calves receive a substantial hydrodynamic advantage, thereby requiring less energy to maintain adult swimming speeds than when swimming alone (Lang, 1966; Weihs, 2004; Noren et al., 2005). In dolphin calves, this energy benefit may be critical to survival. Although most newborn mammals require a disproportionately greater amount of sleep after birth versus later in development, cetacean newborns apparently move continuously for a month

after birth and stop very little in the first several months (Lyamin et al., 2005). The metabolic requirements of continuous movement may have strongly supported genetic and learning mechanisms favoring calf slip-streaming in the form of synchronous mother-calf swimming after birth, including maternal enforcement of the behavior (Fellner & Bauer, unpub. data).

A second advantage of a polarized school or flock moving in synchrony occurs via the sensory integration system (SIS) that allows these animals to act as a single, hypersensitive organism (Norris & Dohl, 1980; Norris & Schilt, 1988). The key to the SIS's heightened abilities is the rapid transmission of information, including acoustic information (cf. Xitco & Roitblat, 1996), from every individual in the school to every other individual. As long as the members of the school are in visual or tactile contact with each other, subtle deviations in the synchronous movements of one or two members may transmit useful information to the rest of the group at a speed more rapid than an approaching predator (the "Trafalgar effect" [Treherne & Foster, 1981] or the "chorus line effect" [Potts, 1984]). Subtle changes in movement or eye gaze are more apparent when the school is tuned to a synchronous rhythm or movement pattern.

Group membership and synchronous movement also offer protection from predators via dilution and confusion effects (Partridge, 1982; Norris & Schilt, 1988; Pitcher & Parrish, 1993; Norris & Johnson, 1994; Roberts, 1996). Solitary animals may be at greater risk simply because within a group there are more targets from which to choose. In addition, moving in unison may contribute to confusion of the predator by causing a visual distraction.

Within cetacean communities, synchrony may be additionally important in social contexts as indicators or reassurances of affiliation, or as a method of initiating, maintaining, or advertising coalitions such as those reported for dolphins (Connor et al., 2000), baboons (*Papio anubis*) (Jolly, 1985), and chimpanzees (*Pan troglodytes*) (Boesch & Boesch, 1989). Norris & Johnson (1994) suggest that mimetic behavior could "initialize" communication among individuals and play a role in relationships within the group. As an expression of affiliation, moving in synchrony may strengthen mother-calf bonds as well as the bonds among male coalitions. Affiliation expressed in this way may also inform other dolphins that certain individuals have an alliance. That synchrony is often observed during other affiliative acts, such as caressing and during bouts of play, which supports this hypothesis (Norris & Johnson, 1994). If it is shown that specific individuals are responsible for maintaining synchrony within a group, then

synchrony may also have implications within hierarchical relationships. A dominant animal may routinely enforce synchronous interactions. For example, Johnson & Norris (1994) observed an intruding spinner dolphin (*Stenella longirostris*) displace a member of a trio and assume synchronous swimming with the remaining two. Alternatively, subordinate animals may initiate synchrony as a display of submission or as a method of gaining favor with more powerful members of the group.

#### *The Role of Synchrony in Imitation*

Synchrony may also play a role in the ontogeny of imitation (Bauer & Harley, 2001; Whiten, 2001). Dolphins have been reported to imitate other species in their environment spontaneously (Tyler & Saayman, 1973). They have demonstrated an ability to imitate humans and conspecifics under experimental conditions (Xitco, 1988; Herman et al., 1993; Bauer & Johnson, 1994; Harley et al., 1998; Xitco et al., 1998; Bauer & Harley, 2001; Herman, 2002). Interestingly, sometimes the imitator begins imitating before the model finishes modeling so that the behaviors are performed simultaneously (Richards et al., 1984; Xitco, 1988; Harley et al., 1998). Furthermore, two dolphins have demonstrated the ability to produce synchronous, unscripted behaviors in response to a "creative tandem" signal (Braslau-Schneck, 1994), a signal to do a new behavior simultaneously. This frequent, spontaneous simultaneity during imitation tasks suggests that synchrony and imitation may have an intimate connection. As synchronous swimming is common in most calves' formative experiences (Fellner et al., 2005), it may be that synchrony is the foundation upon which imitation in dolphins rests.

Evidence for this idea is suggested by acquisition characteristics in imitation paradigms in primates and dolphins. A comparison of imitation studies with children with mental retardation, chimpanzees, and dolphins suggests that dolphins had more natural practice with imitation prior to the beginning of the studies. Chimpanzees took 70 to 140 h of pre-test teaching over a span of 3.5 mo to learn to imitate using the "do-as-I-do" procedure (Custance et al., 1995), a procedure in which a behavior was modeled and the subject was signaled to perform the same behavior. Similarly, two children with mental retardation required mimicry training on over 30 "do-as-I-do" behaviors before they were able to imitate successfully on the first trial (Baer et al., 1967). In contrast, experimental imitation studies of dolphins have revealed that in some cases they imitated immediately (Xitco, 1988; Harley et al., 1998).

In one study, two bottlenose dolphins, about 2 y old, imitated a variety of behaviors modeled by a

human, many on the first trial (Harley et al., 1998; reviewed in Herman, 2002). None of the behaviors had previously been trained, and some were quite novel (i.e., not species typical) such as putting a ball in a basket and retrieving objects and giving them to a trainer. The dolphins in this study did not improve at the “do-as-I-do” paradigm as the study progressed. They began ably and continued well. Furthermore, failures to imitate in this study appeared to be behavior-based (i.e., the behaviors were difficult to perform) rather than conceptually based. For example, one dolphin did not correctly imitate the “through” behavior because she appeared to be afraid of swimming through the hoop; she entered the hoop but then backed out. The immediate success of the dolphins in this study along with their lack of improvement suggested that these young dolphins were doing what came naturally. An interesting characteristic from the standpoint of looking at synchrony as a foundation for imitation was that during many trials in this study, the behaviors were done at the same time. This point leads us to suggest that the dolphins were not arriving at imitation without practice but, rather, that their extensive early experience as calves swimming synchronously with others may have been just the practice they needed to be successful in the “do-as-I-do” paradigm. This practice with synchrony in dolphins served a similar function as the “do-as-I-do” practice trials in primates.

The acquisition of complex behaviors by dolphin calves may fall along a continuum of development. Within seconds of birth, calves in captive settings start moving synchronously with their mothers in stereotyped patterns around their enclosures (Fellner et al., 2005). Initially, the mother maintains synchronous swimming, and the calf is pulled along passively in the mother’s slipstream. As the calf develops, the calf takes a more active role in maintaining synchrony by initiating bouts of synchronous swimming. For the first 4 wks of life, calves swim synchronously with their mothers over 90% of the time. Over the first 3 mo, they swim synchronously with their mothers or other dolphins more than 80% of the time. During this period, both the complexity of synchrony and the calves’ behavioral repertoire increase substantially.

Delay can be considered as an increase in complexity over simultaneous synchronous behavior. In an imitation study similar to the study described with young calves above, Xitco (1988) reported that two 12-y-old experimentally experienced female dolphins were able to perform novel imitative behaviors across a variety of delay lengths thereby preventing them from behaving together. Although accuracy declined as delays lengthened, both dolphins’ performance accuracies were

above chance levels at the longest delays of 80 s. Dolphins may move along a continuum from passive, simple synchronous behaviors to active, simple synchronous behaviors to active, complex synchronous behaviors and, eventually, to imitation. We have direct evidence for the first three stages (Fellner et al., 2005), and we have evidence for imitation after delay. Further study should reveal the intervening stages.

#### *Implications for Future Research*

Dolphin calves begin their lives moving synchronously with their mothers nearly 100% of the time. Older dolphins are capable of learning new behaviors through observation of models. Although calves swim precocially at birth, they are not immediately capable of performing many of the behaviors present in the adult repertoire. Rather, new behaviors appear over time during each calf’s extended period of dependency. A study that explicitly examines the timing of specific behaviors performed by potential models and subsequently by the calf should explicate the pathway to imitation, perhaps through synchrony.

Observations by Johnson & Norris (1994) suggest the following type of behavior that might be investigated in controlled settings for evidence of the role of synchrony in scaffolding and imitation:

*“Aerial behavior is a practiced pattern that seems to require a learning period during the young and juvenile years to be perfected.”*

*We noted that attending alloparents sometimes performed aerial patterns with a young animal, although more often they merely lingered nearby. Whether this represents “instruction” is unknown, but since the coordination between mother and young was sometimes precise, we tend to believe that it might. Such adult-young pairs were sometimes noted swimming in synchrony, breaking the surface in a nearly simultaneous leap. On one occasion, three adults and a young dolphin performed 13 simultaneous arching leaps in a row. (p. 270)*

The problem with observing dolphins in the wild is that most of their behavior takes place out of view. The learning sequences cannot be observed in detail or continuously over the long periods of time that typically characterize learning processes. In a captive setting, dolphins are more easily observed and can often be videotaped on a continuous basis. There, the sequences of behavior acquisition can be carefully analyzed for instances of aerial and other easily observable behaviors.

We also do not know what cues may be important in this potential progression. In a study of imitation, acoustic recordings of the dolphins

suggested that vocalizations or sounds correlated with behaviors may have helped support the dolphins' simultaneous imitative behaviors (Partan & Xitco, unpub. data). In addition, we do not know if vocal imitation, for which there is strong evidence both with captive (Richards et al., 1984; Sigurdson, 1993) and wild (Janik, 1997; Fripp et al., 2005) dolphins, develops from synchronous vocalizations. In one study, when vocal mimicry was delivered in response to computer-generated sounds on command, the subject frequently initiated the response before the end of the model (i.e., a synchronous onset) (Richards et al., 1984). This suggests a possible synchronous route to vocal imitation; however, developmental data are needed to investigate this hypothesis.

From laboratory studies of imitation, it is clear that some individuals are more likely to imitate their partners, and the relationship is not necessarily symmetrical (e.g., Bauer & Johnson, 1994). Dominance relationships are likely to be important in influencing whether an individual will model or imitate another animal. Again, determining the relationship between synchrony, dominance, and willingness to imitate would prove illuminating in predicting how information or behavior is transferred from one individual to another. For example, a study that concurrently measures synchrony characteristics as well as other affiliative or agonistic behaviors may reveal sequences of interactions that initiate, maintain, or terminate affiliative relationships and place synchrony into relational context. In addition, analyses of which individual initiates and terminates bouts of synchrony may be helpful in determining whether the "primary synchronizer" is more likely to be the higher- or lower-ranking individual in a pair. These studies would best be conducted in a facility that had ecologically meaningful social groups.

Moving from action-level (detailed and sequential specific behaviors) imitation in early development to program-level (hierarchical goal-based) imitation (Byrne & Russon, 1998) in later life may be the simplest way to explain within-group, shared behaviors in dolphins like mud-herding (Hoese, 1971; Sargeant et al., 2005), sponging (Smolker et al., 1997; Krützen et al., 2005), and male herding of females (Connor et al., 1992a, 1992b). Hence, cultural exchanges in dolphin communities may ultimately be based in their predisposition for synchrony and the cognitive developments it enables.

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### Literature Cited

- Baer, D. M., Peterson, R. F., & Sherman, J. A. (1967). The development of imitation by reinforcing behavioral similarity to a model. *Journal of Experimental Analysis of Behavior*, 10(5), 405-416.
- Bauer, G. B., & Harley, H. E. (2001). The mimetic dolphin. *Behavioral and Brain Sciences*, 24(2), 326-327.
- Bauer, G. B., & Johnson, C. M. (1994). Trained motor imitation by bottlenose dolphins (*Tursiops truncatus*). *Perceptual & Motor Skills*, 79(3, Pt 1), 1307-1315.
- Bel'kovich, V. M. (1991). Herd structure, hunting, and play: Bottlenose dolphins in the Black Sea. In K. Pryor & K. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 17-78). Berkeley: University of California Press.
- Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78, 547-573.
- Boyd, G. L., & Parsons, G. R. (1998). Swimming performance and behavior of golden shiner, *Notemigonus crysoleucas*, while schooling. *Copeia*, 2, 467-471.
- Braslau-Schneck, S. (1994). *Innovative behaviors and synchronization in bottlenose dolphins*. Unpublished Master's thesis, University of Hawaii, Honolulu.
- Breder, C. M., Jr. (1965). Vortices and fish schools. *Zoologica*, 50, 97-114.
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, 21, 667-684.
- 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). Oxford, UK: Oxford University Press.
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992b). Two levels of alliance formation among male 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.
- Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour*, 132, 837-860.
- Cutts, C. J., & Speakman, J. R. (1994). Energy savings in formation flight of pink-footed geese. *Journal of Experimental Biology*, 189, 251-261.
- Fellner, W., Stamper, S. A., Losch, B. A., Dahood, A., & Bauer, G. B. (2005). *The development of synchrony and*

- behavior in bottlenose dolphins*. Poster presented at the 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA.
- Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., et al. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, 8, 17-26.
- Harley, H. E., Xitco, M. J., Jr., Roitblat, H. L., & Herman, L. M. (1998). *Imitation of human models by bottlenose dolphins*. Poster presented at the Napoli Social Learning Conference, Naples, Italy.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 63-108). Cambridge: MIT Press.
- Herman, L. M., Pack, A. A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. L. Roitblat & L. M. Herman (Eds.), *Language and communication: Comparative perspectives* (pp. 403-442). Hillsdale, NJ: Erlbaum.
- Herskin, J., & Steffensen, J. F. (1998). Energy savings in sea bass swimming in a school: Measurements of tail beat frequency and oxygen consumption at different swimming speeds. *Journal of Fish Biology*, 53(2), 366-376.
- Hoese, H. D. (1971). Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy*, 52(1), 222-223.
- Janik, V. M. (1997). Whistle matching in wild bottlenose dolphins. *The Journal of the Acoustical Society of America*, 101(5), 3136.
- 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: University of California Press.
- Jolly, A. (1985). *The evolution of primate behavior*. New York: Macmillan.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Science*, 102(25), 8939-8943.
- Lang, T. G. (1966). Hydrodynamic analysis of cetacean performance. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 410-432). Berkeley: University of California Press.
- Lyamin, O., Pryaslova, J., Lance, V., & Siegel, J. (2005). Animal behavior: Continuous activity in cetaceans after birth. *Nature*, 435, 1177.
- Matsuzawa, T. (2003). Koshima monkeys and Bossou chimpanzees: Long-term research on culture in nonhuman primates. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity* (pp. 374-387). Cambridge, MA: Harvard University Press.
- Miles, J. A., & Herzog, D. L. (2003). Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquatic Mammals*, 29(3), 363-377.
- Noren, S. R., Biedenback, G., Redfern, J., & Edwards, E. (2005). *The swimming kinematics of mother-calf dolphin pairs: Echelon position reduces the locomotor efforts of calves*. Paper presented at the 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA.
- Norris, K. S., & Dohl, T. P. (1980). The structure and functions of cetacean schools. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 211-261). New York: John Wiley & Sons.
- Norris, K. S., & Johnson, C. M. (1994). Schools and schooling. In K. S. Norris, B. Würsig, R. S. Wells, & M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 232-242). Berkeley: University of California Press.
- Norris, K. S., & Prescott, J. H. (1961). Observations of Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, 63, 291-402.
- Norris, K. S., & Schilt, C. R. (1988). Cooperative societies in three-dimensional space: On the origins of aggregations, flocks and schools, with special reference to dolphins and fish. *Ethology and Sociobiology*, 9, 149-179.
- Partridge, B. L. (1982). The structure and function of fish schools. *Scientific American*, 246(6), 114-123.
- Pitcher, T. J., & Parrish, J. K. (1993). Functions of shoaling behaviour in teleosts. In T. J. Pitcher (Ed.), *Behaviour of teleost fishes* (pp. 363-439). New York: Chapman and Hall.
- Potts, W. K. (1984). The chorus line hypothesis of manoeuvre coordination in avian flocks. *Nature*, 309, 344-345.
- Pryor, K., & Shallenberger, I. (1991). Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the eastern tropical Pacific. In K. Pryor & K. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 161-198). Berkeley: University of California Press.
- Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, 24, 309-382.
- 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(1), 10-28.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, 51, 1077-1086.
- Saayman, G. S., Tayler, C. K., & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus ehrenburg*). *Behaviour*, 44, 212-233.
- Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, 83(11), 1400-1411.
- Sigurdson, J. (1993). Frequency-modulated whistles as a medium for communication with the bottlenose dolphin (*Tursiops truncatus*). In H. L. Roitblat, L. M. Herman, & P. E. Nachtigall (Eds.), *Language and communication:*

- Comparative perspectives* (pp. 153-173). Hillsdale, NJ: Erlbaum.
- 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*, 454-465.
- Taylor, C. K., & Saayman, G. S. (1973). Imitative behavior by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, *44*(3-4), 277-298.
- Thorpe, W. H. (1963). *Learning and instinct in animals*. London: Methuen.
- Treherne, J. E., & Foster, W. A. (1981). Group transmission of predator avoidance behaviour in a marine insect: The Trafalgar effect. *Animal Behaviour*, *29*(3), 911-917.
- Weihls, D. (2004). The hydrodynamics of dolphin drafting. *Journal of Biology*, *3*(2), 8.
- Whiten, A. (2001). Imitation and cultural transmission in apes and cetaceans. *Behavioral and Brain Sciences*, *24*(2), 359-360.
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Advances in the Study of Behaviour*, *21*, 239-283.
- Xitco, M. J., Jr. (1988). *Mimicry of modeled behaviors by bottlenose dolphins*. Unpublished Master's thesis, University of Hawai'i, Manoa.
- Xitco, M. J., Jr., & Roitblat, H. L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Animal Learning and Behavior*, *24*(4), 355-365.
- Xitco, M. J., Jr., Harley, H. E., & Brill, R. L. (1998). *Action level imitation by bottlenose dolphins*. Poster presented at the Napoli Social Learning Conference, Naples, Italy.
- Zentall, T. R. (1998). An analysis of imitative learning in animals. In C. M. Heyes & B. G. Galef Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 211-243). San Diego: Academic Press.