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Observational Learning in Wild and Captive Dolphins

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Many non-human species imitate the behavior of others, and dolphins seem particularly adept at this form of observational learning. Evidence for observational learning in wild dolphins is rare, given the difficulty of observing individual wild animals in sufficient detail to eliminate other possible explanations of purported imitation. Consequently, much of the evidence supporting observational learning in dolphins has involved animals in captive settings. This research suggests that dolphins have an affinity for mimicry, and that they are more successful at observational learning if they choose to imitate another rather than being asked to do so. These results, combined with those obtained from wild dolphins, suggest that imitation may play important roles in the ontogeny of a variety of behaviors, including those involved in communication, foraging, and parenting.

The human capacity for observational learning has been well documented (Bandura, 1997; Meltzoff & Prinz, 2002; Piaget, 1962). This capacity is important because observational learning facilitates the transmission of information from one individual to another (Galef, 2003). Observation of innovative behaviors may speed the acquisition of adaptive novel behaviors in a group and so enhance individual member's chances of surviving and reproducing. In this sense, observational learning, behavioral flexibility, and culture are intertwined. The human capacity for flexibility has resulted in a wide array of cultures. The notion of culture within animal societies remains a matter of considerable debate (e.g., Kuczaj, 2001; Rendell & Whitehead, 2001). But there is general agreement that the behaviors that comprise a culture are maintained through various forms of social learning (Boyd & Richerson, 1996, 2000; Rendell & Whitehead, 2001), one of which is observational learning.

Observational learning comes in a variety of forms (Tomasello, 1999). Local enhancement occurs when individuals become interested in a particular place because they have witnessed another animal at that location. Stimulus enhancement results from an individual watching another interact with an object and then becoming interested in the object. Goal emulation occurs when individuals are intrigued by the end result of an observed behavior. The above are examples of non-imitative social learning in which an animal learns about its environment by observing others (Heyes, 1993). In contrast, imitation occurs when individuals learn about *behavior* from observing others.

There are also different forms of imitation. For example, Kuczaj, Paulos, and Ramos (2005) discussed three types of imitation: (1) kinesthetic, (2) symbolic, and (3) mindful. Kinesthetic imitation occurs when the imitator matches its bodily movements and postures to those of the model. This form of imitation is similar to

Tomasello's (1999) mimicry and Morgan's (1900) instinctive imitation. Symbolic imitation occurs when the imitator must create a lasting representation that stands for the original event. For example, deferred imitation involves the reproduction of behavior that was observed in the past and for which no model is presently available, so it requires that the imitator have a mental representation of the model behavior to produce an imitation (Piaget, 1952, 1962). Mindful imitation occurs when the imitator recognizes and encodes the model's intentions as well as the model's behaviors. Therefore, individuals will reproduce the behavior of a model to achieve the same goal as the model. Mindful imitation is very similar to what Tomasello, Kruger, and Ratner (1993) and Tomasello (1996) referred to as true imitation.

Observational Learning Evidence in Captivity

Some of the best examples of spontaneous observational learning come from captive dolphins, most likely because captive animals can be observed regularly and for long periods of time. Taylor & Saayman (1973) provided some of the best examples of dolphin imitation. In one case, an Indo-Pacific bottlenose dolphin calf (*Tursiops aduncus*) was looking through an underwater window and watching a human smoke a cigarette. The calf swam away, nursed from its mother, returned to the window, and released the milk from its mouth in an apparent attempt to imitate the human's behavior.

Another case from Taylor & Saayman (1973, p. 290) was equally impressive:

The dolphin, after repeatedly observing a diver removing algae growth from the glass underwater viewing port, was seen cleaning the window with a seagull feather while emitting sounds almost identical to that of the diver's air-demand valve and releasing a stream of bubbles from the blowhole in a manner similar to that of exhaust air escaping from the diving apparatus. . . . Subsequently (the dolphin) used food-fish, sea slugs, stones and paper to perform similar cleaning movements at the window.

More recent observations have demonstrated that bottlenose dolphin calves (*Tursiops truncatus*) often spontaneously imitate behaviors, including some they have never produced before (Kuczaj et al., 2005; Kuczaj & Yeater, 2006). Kuczaj and Yeater (2006, p. 417) provided the following example:

For example, one of the calves we observed was rolling his head at the surface of the water and creating waves, a behavior we had not witnessed before. While the calf was producing this behavior, another calf joined him and began to mimic the first calf's behavior. In some cases, imitation was deferred, with the imitations occurring some time after the model behavior had been observed (ranging from 15 min to 3 d). For example, a young calf watched its mother blow individual bubbles, after which the mother bit

each of the bubbles. The calf had not produced this behavior before, but approximately 45 min after watching its mother do so, the calf blew some small bubbles and bit a few of them.

Another observation involved a calf playing with a football, the solitary game consisting of releasing and retrieving the football in a submerged box under the dock. Other dolphins appeared interested in this behavior, and within a few days another calf and three adults were engaging in this activity as well (Kuczaj et al., 2005). Pryor (1975) also reported other cases of novel behaviors spreading among captive dolphin populations, such as seaweed carrying and balancing on the edge of the tank.

Dolphins' apparent predisposition to imitate others may result from their ability to spontaneously synchronize their behaviors (Bauer & Harley, 2001). Fellner, Bauer, and Harley (2006) suggested that the evolutionary foundation of dolphin imitation is established early in a dolphin calf's life through mom-calf synchronous behaviors, especially synchronous swimming. Dolphin calves have extensive experience swimming synchronously with their mothers, which may facilitate the "do-as-I-do" imitation paradigm.

Yeater (2005) observed a dolphin calf that learned to voluntarily regurgitate pieces of fish through observational learning. The calf had been stranded, rehabilitated in isolation, and then introduced into a social group of captive dolphins all within a few months time span. The calf observed other dolphins that regurgitated and played with fish, and appeared to learn to regurgitate fish by watching others, especially by closely observing another juvenile female. Although the calf seemed intrigued by this behavior, she did not regurgitate fish until several months later. This suggests that the calf was representing the other's regurgitation behavior and using these representations to later reproduce such behaviors herself. Thus, this was an example of deferred imitation (Kuczaj & Yeater, 2006; Piaget, 1952), demonstrating that imitation need not be immediate. Yeater (2005) also reported that voluntary regurgitation within this captive group of dolphins appeared to be maintained by the reinforcement of producing their own play item, a regurgitated fish. Other studies have similarly reported that young dolphins frequently spontaneously imitate the play behaviors of their peers, and sometimes acquire novel play behaviors in the process (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Kuczaj & Yeater, 2006).

Some models are more likely to be imitated than others (Bandura, 1986; Kuczaj & Yeater, 2006). Dolphin calves are more likely to imitate other calves than they are to imitate adults, including their mothers (Kuczaj et al., 2006). Context is likely an important determinant of who is imitated. Dolphin calves are more likely to imitate peers in a play context, but they might be more likely to imitate their mothers in a foraging context. However, even among calves, some models are more likely to be imitated. Young dolphins are more likely to imitate older (and more competent) peers than younger, less competent peers.

Observational Learning Evidence from the Wild

Despite the inherent difficulties of assessing various forms of observational learning in wild dolphins, there are observations that suggest spontaneous mimicry in wild dolphins. For example, K. Sexton (personal communication, 2005) observed an occasion of apparent imitation in the wild. His observation was described as follows by Kuczaj & Yeater (2006, p. 417):

He observed two bottlenose dolphins (that he believed to be Tursiops gilli) bow riding, one of which was a juvenile. The adult dolphin performed a barrel roll and then turned its head toward the juvenile. The adult repeated this behavior several times, after which the juvenile attempted a barrel roll, but lost its position on the pressure wave while doing so. The adult immediately left, but both animals returned within a few minutes. The adult then performed two barrel rolls, looking toward the juvenile after each roll was completed. The juvenile again attempted a roll, and once again fell off the wave. The adult followed, and both animals quickly returned to the wave. The adult produced one roll following their return, after which the juvenile attempted a roll, once again losing its position in the wave. The adult did not follow the juvenile this time, and the juvenile soon returned. At this point, the juvenile completed a roll and managed to stay on the wave, after which it looked toward the adult. It then produced several successive rolls in a row.

Dolphin calves also seem to learn certain foraging strategies by observing their mothers (Boran & Heimlich, 1999; Sargeant & Mann, 2009). For example, bottlenose dolphins use various types of synchronous behaviors in the wild in order to catch prey. Bottlenose dolphins in Shark Bay, Australia perform “kerplunking,” or a loud splash with their tails, as a foraging strategy that may stun prey (Connor, Heithaus, Berggren, & Miksis, 2000). This behavior was first observed in an adult female and appeared to serve as a signaling function to attract the attention of her calf. Another small population of female bottlenose dolphins in Shark Bay, Australia regularly engaged in sponge carrying as a behavioral specialization, an apparent foraging strategy in which the sponges are used to prevent injury as dolphins use sponges on the tips of their rostrums to search the ocean floor for prey (Smolker, Richards, Connor, Mann, & Berggren, 1997). This behavior is sometimes transmitted from mother to calf, and most often to daughters. The precise form of observational learning that is involved in this transmission is unknown (Krutzen, Mann, Heithaus, Connor, Bejder, & Sherwin, 2005). Sargeant and Mann (2009) found that social learning is evident in the ontogeny of foraging strategies in bottlenose dolphins at Shark Bay, Australia. The evidence from several maternal foraging strategies (sponge carrying, mill foraging, and rooster-tail foraging) suggested that vertical social learning (mother-to-offspring) was most common. This indicated the dominance of a ‘do-what-mother-

does' strategy, rather than one of simply copying the foraging behavior of conspecifics of all ages.

Bender, Herzog, and Bjorklund (2009) found that Atlantic spotted dolphin mothers (*Stenella frontalis*) used observational learning to teach their calves foraging techniques. Nine mothers chased prey for longer periods of time and made more referential body pointing movements while foraging when naive calves were present; such behaviors provide extended opportunities for the calves to observe the mother's behavior. In addition, when mothers were foraging with their attentive calves, the mothers sometimes would let the prey escape and burrow into the sand before recapturing the prey, and even allowed calves to chase the prey. Although the mothers in these events altered their foraging strategies to prolong the foraging event, they never lost the prey. The mothers, then, seemed to have control over the prey, which they used to also capture their calves' interest, the result being a rich opportunity for the calves to learn foraging behaviors by watching the mother and sometimes even practicing foraging behaviors themselves.

Killer whales (*Orcinus orca*) in the Crozet Islands and off Punta Norte, Argentina capture seal pups by intentionally stranding on breeding beaches (Guinet & Bouvier, 1995). Adult females modified their stranding behavior in the presence of naive juvenile calves, suggesting that females were providing the calves with opportunities to observe various stranding techniques that could be used to capture seal pups. Guinet (1991) suggested that killer whale calves developed intentional stranding foraging skills through imitation of the successful hunting behaviors of their mothers (or other relatives).

Conclusions

The dolphin capacity for observational learning is widely recognized (Kuczaj & Yeater, 2006; Marino et al., 2007). Dolphins have also demonstrated a vast capacity for imitation, viewed by many as one of the highest forms of social learning (Kuczaj et al., 2005; Tomasello, 1996, 1999; Tomasello et al., 1993). This has even led a leading primatologist, Andrew Whiten, to acknowledge that dolphins "ape better than apes" (Whiten, 2001). Although we have focused on spontaneous observational learning in this paper, much of what is known about the dolphins' capacity for imitation comes from studies of captive animals that have been asked to imitate another's behavior (or their own behavior; see Kuczaj & Yeater, 2006, for a consideration of this work). It is impossible to ask wild dolphins to imitate, and so the elicited imitation technique used with captive dolphins has provided valuable information that could not be obtained from wild animals. Although observations of spontaneous imitation come from both wild and captive populations, more information about an individual animal's behavioral history and observational opportunities is typically available from a captive animal than a wild one, a result of the difficulties inherent in field research compared to captive research. This means that it is often easier to determine the type of observational learning that has occurred in a captive setting, although this is not

always possible given that even captive animals are not constantly observed. Clearly, the dolphins' capacity for observational learning is a reflection of their capacity for flexible thinking, and undoubtedly plays an important role in the transmission of information from dolphin to dolphin. The exact nature of this role will only be determined by additional studies of various forms of observational learning in both captive and wild settings.

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