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Title

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Journal

International Journal of Comparative Psychology, 19(2)

ISSN

0889-3675

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Publication Date

2006-12-31

DOI

10.46867/ijcp.2006.19.02.02

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Peer reviewed

Role of Peers in Cultural Innovation and Cultural Transmission: Evidence from the Play of Dolphin Calves

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Observations of the spontaneous play behaviors of a group of captive bottlenose dolphins (*Tursiops truncatus*) revealed that each individual calf's play became more complex with increasing age, suggesting that dolphin play may facilitate the ontogeny and maintenance of flexible problem solving skills. If this is so, play may have evolved to help young dolphins learn to adapt to novel situations. Novel play behaviors were more likely to be produced by dolphin calves than by adults, demonstrating that calves were the main source of innovative play behaviors in the group. Calves were also more likely to imitate novel play behaviors first produced by another dolphin, suggesting that calves contribute significantly to the spread of novel behaviors within a group. All in all, these data suggest that peers may be important catalysts for both cultural innovation and cultural transmission, and that the opportunity to interact with peers may enhance the effect play has on the emergence of flexible problem solving skills.

Although notoriously difficult to define, play has captivated the interest of many scholars (e.g., Burghardt, 2005; Groos, 1898, 1901; Piaget, 1951; Vygotsky, 1978). Many discussions of play note that play appears purposeless (at least in terms of immediate consequences) and typically consists of behaviors that may appear in other contexts, such behaviors being modified during play in terms of both form and temporal sequencing (e.g., Bekoff & Byers, 1981). Although play may appear purposeless, many theorists consider it an important aspect of development that helps young organisms acquire behaviors and abilities that facilitate their survival. These benefits of play may be immediate or delayed, depending on the organism and the type of play (Burghardt, 2005; Pellegrini & Bjorklund, 2004).

Humans seem better at recognizing play than at defining it. Behaviors characterized as play have been observed in the young of most mammalian species, as well as some bird and reptile species, a finding that has led to considerable speculation about play's significance for both phylogeny and ontogeny (Bekoff & Byers, 1981; Burghardt, 2005; Dugatkin & Bekoff, 2003; Fagen, 1981; Ficken, 1977; Jewell & Loizos, 1966; Ortega & Bekoff, 1987; Pellegrini & Bjorklund, 2004; Spinka, Newberry, & Bekoff, 2001). Given the ubiquitous nature of play in many young animals, it seems likely that selection pressures may have contributed to the evolution of play behavior in animals (Burghardt, 2005; Fagan, 1981; Lancy, 1980; Martin & Caro, 1985; Pellegrini & Bjorklund, 2004; Power, 2000). Play was most likely selected for because it helps animals gain knowledge of the properties of objects, perfect motor skills, and recognize and manipulate characteristics of their environment (Bekoff & Allen, 1998; Bornstein & O'Reilly, 1993; Bruner, 1972, 1973; Fagen, 1981; Garvey, 1974; Groos, 1898; Piaget, 1951; 1952; Vandenberg, 1978). Play also facilitates the development of flexible problem solving

skills by providing a context in which animals can explore the consequences of new behaviors and even produce their own moderately discrepant events (Kuczaj & Trone, 2001; Spinka, Newberry, & Bekoff, 2001). In such cases, the playing animal creates situations that are both somewhat familiar and somewhat novel, the result being a more challenging play context than one that the animal has already mastered. Play allows an animal to freely alternate easy and difficult tasks, and so provides opportunities for innovation that might not exist in other behavioral contexts.

Play can be solitary or social. Many animals, including social animals, engage in solitary play. In fact, young human children are more likely to engage in certain forms of language play when they are alone than when they are with others (Kuczaj, 1982, 1983; Weir, 1962). Such play appears to facilitate aspects of language development, demonstrating that play need not be social to influence development. However, social play may be particularly important for certain aspects of development (Bekoff, 2001). Social play often involves role reversals in which a dominant animal and a subordinate animal switch dominance relations, a phenomenon that is only observed during play. Social play helps young animals learn about other members of their group and may even determine enduring social relationships among the players (Bekoff & Byers, 1981; Coelho & Bramblett, 1982; Colvin & Tissier, 1985; Guinet, 1991; Miller & Nadler, 1982; Thompson, 1996; Walters, 1987). In addition, social play facilitates the development of an animal's behavioral repertoire, assisting in the acquisition of behaviors necessary to succeed in a variety of non-play contexts (Coelho & Bramblett, 1982; West, 1974). All in all, then, social play provides a context in which considerable social learning may occur.

By definition, social learning results in the social transmission of behaviors through some form of social interaction, such as observation of a model (see, e.g., Box, 1984; Boyd & Richerson, 1988; Russon, 1997). Social learning may result in the spread of new behaviors that are initially produced by a single individual. Examples include the changes in humpback whale songs when a group is exposed to a new version (Noad, Cato, Bryden, Jenner, & Jenner, 2000), the gradual emergence of sweet potato washing, wheat-washing, and stone play among members of macaque troops (Huffman, 1984; Itani & Nishimura, 1973; Kawai, 1965), and tongue piercing by American adolescents. However, some behaviors are more likely to be reproduced than others. Human children (and adults) are more likely to imitate behaviors that have been reinforced (Bandura, 1977). In addition, children are more likely to imitate models with whom they have a significant relationship, such as kin or friends (Yando, Seitz, & Zigler, 1978). This is also true for at least some animals. Russon and Galdikas (1995) reported that orangutans were more likely to imitate models (orangutans or humans) with which the animal had an established relationship. Thus, although behaviors can be transmitted across generations or within generations (Jones & Kamil, 1973; Kawai, 1965), the likelihood that an observed behavior will be acquired depends at least in part on the significance of the model for the observer.

For many species, peers are significant individuals for a young animal. Peers are often the first creatures other than the mother with whom young animals interact (Poirer, 1970). Normal behavioral development may require sufficient opportunities for peer interaction, especially early in the developing animal's life

(Bekoff, 1972). Peer interactions may even counteract the negative consequences of early separation from the mother (Harlow, 1969; Tisza, Hurwitz, & Angoff, 1970). Some species have demonstrated preferences for peers as play partners. Belding's ground squirrels (*Spermophilus beldingi*) and voles (*Microtus* spp.) are more likely to play with littermates than other animals (Holmes, 1994; Wilson, 1982). Red-necked wallabies (*macropus rufogriseus*) prefer play partners of the same sex and social status (Watson, 1993), but chimpanzees (*Pan troglodytes*) prefer play partners that are either younger or older than themselves and are equally likely to play with peers of either sex (Markus & Croft, 1995). But how influential are peers in the cultural transmission of behavior?

In order to answer this question, we examined the roles of peers in the ontogeny of spontaneous play behaviors among a group of captive bottlenose dolphins (*Tursiops truncatus*). Dolphins are good subjects for investigations of play, since play occurs in dolphins of all ages, both in captivity and in the wild (Baird & Dill, 1995; Bel'kovich, Ivanova, Kozarovitsky, Novikova & Kharitonov, 1991; Delfour & Aulagnier, 1997; Essapian, 1953; Gewalt, 1989; Guinet, 1991; Kuczaj & Walker, 2006; Payne, 1995; Marten, Shariff, Psarakos, & White, 1996; McCowan, Marino, Vance, Walke & Reiss, 2000; Pace, 2000; Sylvestre, 1985; Würsig, Dorsey, Richardson, & Wells, 1989). Dolphins play with items such as balls and buoys that are given to them, items such as feathers and seaweed that they find in their environment, and items such as bubbles or bubble rings that dolphins themselves create. They play with these items in various ways, such as throwing them in the air, pushing them with various parts of their bodies, or combining objects in unique ways (e.g., placing a ball in a box). Early anecdotal observations suggested that the play behavior of young dolphins in captivity was characterized by their creativity (McBride & Hebb, 1948; Tavalga, 1966), reports that are consistent with our observations of dolphin play (Kuczaj & Trone, 2001; Kuczaj & Walker, 2006).

Although individual animals produce novel play behaviors that are initially present only in their repertoire, social learning may result in other animals acquiring similar behaviors. Peers may be particularly salient for some species and so influence both the amount and types of play behaviors in which young animals engage (Huffman, 1984; Kuyk, Dazey, & Ervin, 1976; Pace, 2000). For example, Pace (2000) reported that two dolphin calves imitated each other's novel sequences of fluke-made bubble rings, and Huffman (1984) reported that stone play in a group of Japanese macaques was originally transmitted only among peers. These findings are consistent with the notion that peers are particularly salient models of novel behaviors. However, the presence of peers does not always result in social learning. Kuyk et al. (1976) reported that infant pigtail monkeys (*Macaca nemestrina*) were more likely to engage in non-social play with objects when peers were present, and speculated that the presence of peers may have enhanced self-awareness in the young monkeys, this heightened sense of awareness resulting in increased attention to the inanimate objects in the environment, and thereby more solitary object play. Regardless of the veracity of this suggestion, the infant monkeys did not seem to learn play behaviors from one another in this context.

We wished to explore the possibility that dolphin calves facilitate both innovation and transmission of novel behaviors in a dolphin group. To do so, we

analyzed novel play behaviors that occurred among a group of captive dolphins studied over a five year period.

Method

Subjects

The animals in this study were sixteen captive bottlenose dolphins (*Tursiops truncatus*) housed in a pool 90' in diameter and 20' deep located at Marine Life Oceanarium in Gulfport, Mississippi. Sixteen dolphins were observed over a five year period (1997-2001). This sample consisted of seven adults (six females and one male, each fifteen years of age or older when the study began) and nine calves/juveniles (seven males and two females). Four of the calves (three males and one female) were born approximately six months prior to the onset of this study. The remaining five calves were born during the study period: one male calf was born in 1997, one female in 1998, two males in 1999, and another male in 2001. The social dynamics of the dolphin group changed during the course of the study period as the result of the births of calves, the death of one adult female, and the movement of dolphins from one tank to another. The particulars for each dolphin are shown in Table 1.

Table 1
Dolphin Characteristics

Dolphin	Adult/Calf	Birth Date	Sex
CBA	Calf	6/96	Male
CNA	Calf	6/96	Female
CPO	Calf	6/96	Male
CBR	Calf	5/96	Male
CJA*	Calf	6/97	Male
CKA*	Calf	9/98	Female
CNO*	Calf	3/99	Male
CJO*	Calf	3/99	Male
CEL*	Calf	4/01	Male
ABA	Adult	unknown	Male
ACA	Adult	unknown	Female
ACH	Adult	unknown	Female
AJA	Adult	unknown	Female
AJI	Adult	unknown	Female
AKE	Adult	unknown	Female
ASH	Adult	unknown	Female

Note: *Observed during first six months of life

Procedure

Behavioral ethograms were constructed with the goal of assessing each animal's behavior, including solitary behaviors, social behaviors, and play behaviors. The ethograms consisted of lists of target behavioral categories and sampling procedures used to insure systematic data collection (see Mann, 2000, for a discussion of the use of ethograms in marine mammal research). Both scan sampling and *ad libitum* sampling were used in the present study. The scan sampling consisted of recording each dolphin's behavior every 5 minutes for a 30 minute observation period. This technique resulted in each animal's behaviors being recorded equally often during each observation period. The *ad libitum* sampling involved recording all observed behaviors from as many animals as possible during the same 30 minute observation period. This sampling approach provided detailed information about the behavior of individual animals, but also occasionally resulted in the behaviors of some animals being sampled at higher rates than others. The combination of scan sampling and *ad libitum* sampling allowed us to take advantage of the strengths of each approach. Scan sampling insured equal numbers of observations of each animal during observation periods, while *ad libitum* sampling allowed observers to record interesting behaviors that might have been missed otherwise (see Altmann, 1974, and Mann, 2000, for discussions of the strengths and weaknesses of these sampling techniques).

On average, six observations were collected per week during the five year sampling period. Each observation was thirty minutes in duration. Given that the observations took place in a public facility that produced several dolphin shows each day, certain restrictions were placed on the observations. Observations ended a minimum of fifteen minutes before a show began and started no sooner than fifteen minutes after a show ended in order to minimize any behavioral biases that might have resulted from either dolphin anticipation of a show or the aftermath of a show performance. All observations were taken during daylight hours, but the time of each observation was randomly determined other than the restrictions due to show performances.

Behavioral Play Categories

Dolphin play behaviors were coded in terms of five general categories: ball play, object play (with objects other than balls), bubble play, human play, and motor play. *Ball play* occurred when a dolphin manipulated one or more of a number of balls which were placed in the tank each day. Examples included holding the ball, swimming and tossing the ball simultaneously, using the mouth or chin to dribble the ball at the surface of the water or under the water, pushing the ball with a body part, trapping the ball between a hard surface and part of the body, using the ball as a rubbing tool, and placing the ball into enclosed spaces and then releasing it. *Object play* involved behaviors similar to those in ball play, but with objects other than balls. We made this distinction because the dolphins played with balls much more often than with other types of objects, and so felt it was important to distinguish ball play from other forms of object play. *Bubble play* occurred when a dolphin manipulated the bubbles another dolphin had produced or played with its own self-produced bubbles. *Human play* consisted of a dolphin interacting with a human in some playful context. This typically involved balls or other objects, as when a dolphin and a human tossed a ball back and forth to one another. *Motor play* involved activities produced by the dolphin that did not involve a movable object, such as fluke walks, spiral swims, or beaching oneself on a dock. All play behaviors were spontaneously produced by dolphins and were never reinforced by dolphin trainers with fish or praise. Although it is possible that dolphin play was reinforced by other dolphins or by humans when dolphins engaged in interactive play with humans (throwing the ball back to a dolphin may have reinforced the dolphin that had just tossed the ball to a human), but it is clear that the behaviors were not trained in the same manner as show or husbandry behaviors.

Play behaviors were considered novel only if they had not been previously produced by one of the dolphins. For example, dolphins were swimming while tossing a ball when our observations began, and so although each calf learned to toss a ball while swimming, the ontogeny of such behavior for a calf was not considered an example of a novel play behavior. But if a calf later produced a behavior with the ball that no other dolphin had been observed performing (such as tossing the ball against the wall of the pool and catching it in its mouth on the rebound), this was considered an example of a novel behavior. Although some forms of novel play were variations of existing behaviors, others consisted of dolphins performing behaviors quite different from any ever seen before. For example, one calf discovered via trial and error over the course of an afternoon that it could take a football under one of the docks in its tank, carefully position the ball with one of its pointed ends

aimed toward an opening in a box built on the bottom of the dock, and release the ball, resulting in the football becoming lodged in the box. On another occasion, a calf learned how to toss a large wooden disk across the surface of the water so that it quickly skimmed the surface of the water, which initially startled the other calves that had been observing his play, but subsequently intrigued them. In this case, the calves regrouped behind the disk-tossing calf and watched his subsequent attempts to “skim” the disk across the surface of the water.

For the sake of this study, novel behaviors were excluded from subsequent analyses if more than one animal was observed producing the behavior when it was first observed. This rarely occurred, but such occurrences made it impossible to determine which animal had created the new form of play. In all other cases, the identity of the innovator was noted. If the innovator was a calf, the age of the calf at the time the behavior was first observed was noted. If the behavior spread among the dolphin group, the identities of the mimicking dolphins and the date on which the animals first reproduced the previously modeled behavior were noted. Of course, the animal that originally created a novel play behavior may not have intended to produce a behavior for other dolphins to mimic, and we use the phrase “modeled behavior” as convenient shorthand to indicate that an animal first produced a behavior that was later produced by another animal.

At this point, it is important to distinguish our results from those reported by Pryor, Haag, & O’Reilly’s (1969) report on the production of novel behaviors by dolphins. In their study, rough-toothed dolphins (*Steno bredanensis*) were trained to produce novel behaviors on command, and were reinforced for doing so. This procedure resulted in significant increases in novel behavior, and demonstrated that the dolphins could remember behaviors that they had already performed and could learn to produce behaviors for which they had not previously been reinforced. This is impressive, but differs in important ways from the novel forms of behavior we observed. First, the dolphins in our study were not trained to produce novel behaviors, but instead, did so spontaneously. Second, although the novel behaviors produced by the dolphins in the present study may have been reinforced in some way by others (e.g., increased attention by other dolphins) or may have been intrinsically reinforcing in some sense, the dolphins were never directly reinforced by trainers following a novel play behavior.

Results

The number of unique play behaviors that occurred within each general play category is shown in Table 2. The dolphins produced 317 distinct forms of play behavior during the five years that they were observed. Thirty-seven of these behaviors were observed during the initial phases of our observations and so were considered existing play behaviors. The remaining types of play behaviors were created by dolphins during the course of this study, and so considered novel play behaviors. Of these, it proved impossible to determine the individual animal responsible for the initial appearance of ten behaviors. As shown in Table 2, play behaviors were not equally distributed across the five general play categories. Dolphins were much more likely to engage in play involving balls or objects than play involving bubbles, humans, or motor activities alone ($X^2(4) = 467.09, p < 0.001$).

With increasing age, play became more complex for each calf. For example, Table 3 shows the ages (in days) at which three dolphin calves were first observed producing five types of ball play. Each calf swam while tossing a ball at a younger age than they produced other target ball play behaviors. One calf (CJA) did so 155 days before he tossed the ball onto a dock or off a wall, 255 days before he swam upside down while tossing the ball, and 474 days before he tossed the ball out of the pool. Another calf (CJO) exhibited a similar developmental pattern, but at an accelerated developmental pace. The remaining calf (CKA) produced the four more complex ball behaviors shortly after she learned to swim and toss the ball. Thus, even though dolphin play behaviors became more complex with increasing age, there was considerable individual variation in the rate of development. The opportunity to interact with and observe older calves may have influ-

enced these individual differences. CJA had limited opportunities to interact with other calves during his first six months of life due to his mother's protective nature. She rarely let him leave her side, and as a result, he was rarely able to play with the older calves in the tank (which were moved to another tank when he was six months old). In contrast, CKA frequently interacted with CJA and appeared to learn complex play behaviors from interacting with and observing him. Similarly, CJO was able to freely interact with two older calves (CJA and CKA), and tended to produce ball play behaviors at much younger ages than either of the older calves had, perhaps because CJO benefited from observing their ball play.

Table 2
Number of Different Play Types that Occurred within each Play Category.

Type of Play	Number of play types within a general play category
Motor	5
Bubble	9
Human	10
Ball	93
Object	200
Total	317

Table 3
Age (in days) that Three Calves Produced Different Types of Ball Play Behaviors.

	Swim & Toss	Toss on dock	Toss off wall	Upside-down swim & toss	Toss out of pool
CJA	133	278	278	378	607
CKA	143	151	155	157	157
CJO	98	105	119	124	184

The notion that older calf models facilitated the ontogeny of play behaviors is supported by other data as well. Figure 1 shows the ages at which three calves were first observed biting individual bubbles they had produced underwater and the ages at which they were first observed biting bubble rings they had produced underwater. These data revealed an inverse relationship between birth order and age of acquisition. The first-born of these three calves (CJA) began to produce both types of play behaviors at much later ages than did either of the younger calves. The youngest calf (CEL) began to bite individual bubbles and bubble rings

at younger ages than had his two older peers. The middle calf fell somewhere in between these two extremes.

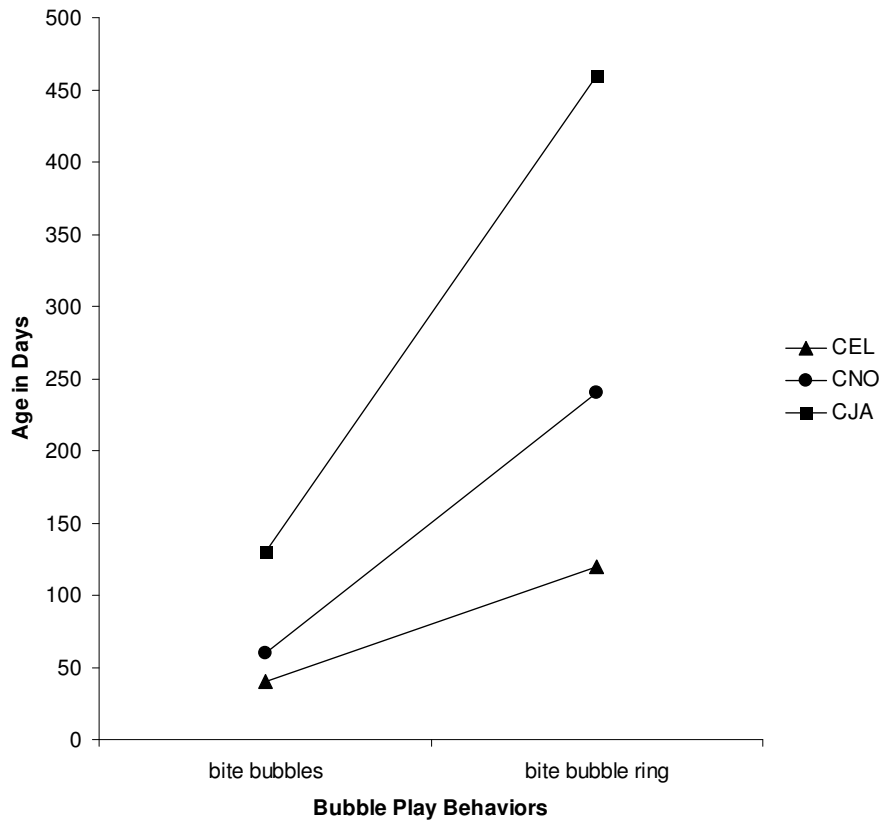


Figure 1. Age at which three calves first produced two bubble play behaviors.

The significance of older calf models was also evident in comparisons of the number of novel play types produced by each of the five calves during the first six months of life. As shown in Table 4, dolphin calves that had two or more older calves in the tank with them during the first six months of life produced more types of novel play behaviors than did calves that were raised without the benefit of older peers. However, the case of CJA shows that the mere presence of other calves was insufficient. He was raised with four older calves in his environment, but was actively discouraged by his mother from interacting with these older calves. Thus, the opportunity to interact with other calves seems necessary to facilitate the ontogeny of complex play behaviors.

There were a total of 270 novel play behaviors in which the initiating dolphin could be identified. These novel play behaviors included novel behaviors with familiar objects, generalizations of existing behaviors to novel objects, and novel behaviors with novel objects. The following are examples of novel behaviors with familiar objects: Swimming upside down on the surface of the water while holding a ball between the pectoral fins; jumping in the air and landing on a ball; using the fluke to pin the ball against the bottom of the pool; dribbling the ball on the bottom of the pool; using the fluke to hit bubbles that had just been released; and swimming under a bubble ring that had just been produced and releasing bubbles that

pass through the ring. Generalizations of existing behaviors to new objects included: swimming while tossing a buoy; swimming while holding a small plastic bucket under one pectoral fin; tossing a pair of sunglasses (that had fallen into the pool) into the air and catching them with the mouth; and attempting to dribble (unsuccessfully) a water-filled ball while swimming on the surface of the water. The following are examples of novel behaviors with novel objects: the dolphin that had attempted to dribble a water-filled ball at the surface began to drop the ball at the surface and then catch it with different parts of its body before the ball hit the bottom of the pool; a dolphin that had retrieved a feather stationed herself in front of an underwater stream of water that flowed into the pool, released the feather so that it initially floated away from her and was caught in the stream, which brought the feather back to the dolphin; a dolphin had a nylon scarf in its mouth while swimming, which it then released and caught on one of its pectoral fins, followed by letting it go again and catching it with its fluke.

Table 4
Number of Different Play Behaviors Exhibited by Five Calves.

Calf	Birth Date	Number of novel play types
CJA	6/97	22
CKA	9/98	28
CNO	3/99	47
CJO	3/99	44
CEL	4/01	62

As shown in Figure 2, calves were more likely than adults to be the animal to first produce a new behavior ($\chi^2(1) = 68.5, p < 0.001$). Specifically, calves were responsible for 220 (81.4%) of the 270 novel play behaviors. Of the 270 novel behaviors, 163 were subsequently reproduced by another dolphin. As also shown in Figure 2, calves were more likely than adults to mimic the original behavior ($\chi^2(1) = 9.87, p < 0.01$). For example, a calf was observed catching in its mouth drops of water that were falling off the roof rafters during a rain storm. Another calf watched for several minutes and then began to catch the falling water drops in her mouth. On another occasion, a calf had beached itself on a dock and slapped the water with its fluke as it reentered the pool. Shortly thereafter, another calf mimicked this behavior. The above examples illustrate behaviors that were mimicked by one or only a few individuals. Other novel behaviors spread more quickly throughout the group, although no novel behaviors were acquired by *every* dolphin in the group. For example, one calf learned to hold the ball between its pectoral fins while swimming and to release the ball in such a way that it caught the ball under its “chin”, followed by the calf “dribbling” the ball underwater. Over the next two months, five of the other seven dolphins in the tank at that time produced the same behavior. The first animal to mimic this behavior was an adult female

(not the calf's mother). Although calves were more likely than adults to mimic novel play behaviors, most adults did mimic at least the occasional play behavior. The sole exception was an adult female that was never observed mimicking another dolphins' play. The female was one of the dominant animals in the tank, and did engage in frequent play with balls. However, she never mimicked another dolphin's novel ball play.

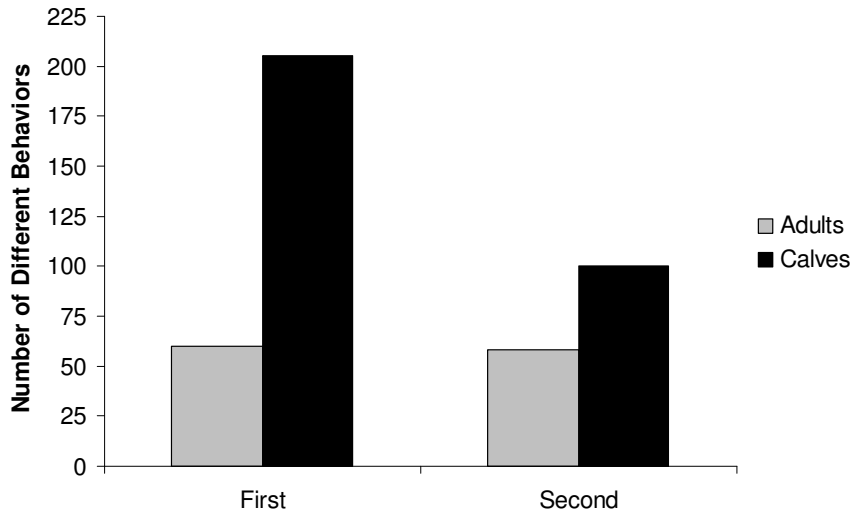


Figure 2. Number of behaviors that were produced first or second by adults or by calves.

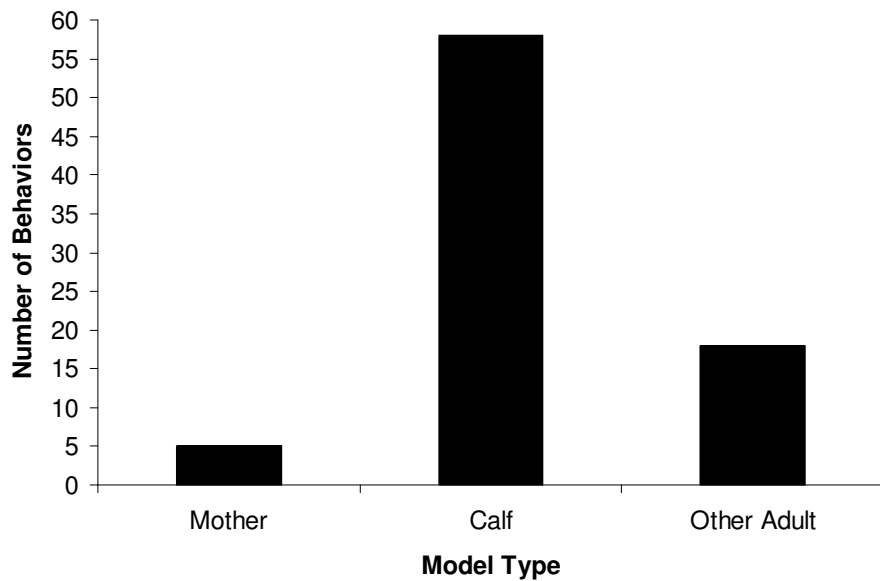


Figure 3. Calf imitations of novel behaviors, categorized by model that was imitated.

At this point, it is important to note that all of the calves had models other than peers from which to learn play behaviors. For example, every adult dolphin played with balls, and so various forms of ball play were modeled by adult dol-

phins as well as other calves. However, adults proved to be less significant models than did other calves (Figure 3). In fact, both adults and calves were more likely to imitate novel play behaviors produced by calves than by adults $t(11) = 4.6$; $p < 0.001$. The age of a calf did not determine the likelihood that its novel behaviors would be reproduced by others. Although older calves were slightly more likely to be imitated than were younger calves, this difference was not statistically significant. Calves were more likely to imitate novel forms of play produced by animals other than their mother than they were to imitate novel forms of play produced by their mother $t(8) = 2.8$; $p < 0.05$. Even when the imitation of other calves was removed from the analysis, calves were more likely to imitate the novel play behaviors of adults other than their mother $t(8) = 2.9$; $p < 0.05$. The mother mentioned above that never mimicked other dolphins' play behaviors rarely produced novel play behaviors, and so was never mimicked in this context. Thus, she neither mimicked nor was mimicked insofar as novel play behaviors were concerned. Of course, it is not clear if her more typical play behaviors were mimicked by calves as they learned to play with balls. Given the relatively high frequency of such behaviors in the group repertoire, it is difficult to determine which animal a calf was mimicking as it acquired such behaviors.

Discussion

Play is common in young dolphins, and is likely an important aspect of dolphin behavioral development. The results of the present study show that dolphin play becomes more complex with increasing age, and suggests that the play process is more important than the play product (see also Kuczaj & Walker, 2006; Rubin, Fein, & Vandenberg, 1983). For example, CJA's ball play occurred in the following sequence: touch ball with his rostrum (nose), mouth ball, carry ball in mouth, toss and retrieve ball, toss ball to humans, hit ball with fluke (tail), hold ball with pectoral fin(s), take ball to bottom of pool and release, swim upside-down and toss ball, toss ball over dock, and toss ball out of pool. Although this sequence took place over the course of two years, each of these behaviors was quickly generalized to a novel object (a small buoy) that was placed into the tank. CJA was clearly learning from his play.

Piaget (1952) suggested that moderately discrepant events are essential aspects of cognitive development for human children. Such events are both familiar and novel (hence the phrase "moderately discrepant"), and so provide a familiar basis for interpreting novel information. At the same time, the novel aspect of a moderately discrepant event requires the organism experiencing the event to learn something new if it is to understand the event. If the organism learns something new, then cognitive development occurs. Our observations suggest that dolphins use play to create their own moderately discrepant events, and so enhance their cognitive development by providing themselves with stimulating environments. For example, one calf became proficient at blowing bubbles while swimming upside-down near the bottom of the pool and then chasing and biting each bubble before it reached the surface of the water. She then began to release bubbles while swimming closer and closer to the surface, eventually being so close that she could not catch a single bubble. During all of this, the number of bubbles released was varied, the end result being that the dolphin learned to produce different numbers

of bubbles from different depths, the apparent goal being to catch the last bubble right before it reached the surface of the water. She also modified her swimming style while releasing bubbles, one variation involving a fast spin-swim. This made it more difficult for her to catch all of the bubbles she released, but she persisted in this behavior until she was able to catch almost all of the bubbles she released. Curiously, the dolphin never released three or fewer bubbles, a number which she was able to catch and bite following the spin-swim release. Although it is possible that she could not release fewer than four bubbles during a spin-swim, she was able to release single bubbles in other contexts. Perhaps the dolphin was keeping her play interesting by producing more bubbles than she could easily catch and bite in this context. These observations are consistent with the notion that play facilitates the development and maintenance of flexible problem solving skills. If this is true, play may have evolved to enhance the ability to adapt to novel situations (Kuczaj & Trone, 2001; Spinka et al., 2001), an important ability for species that inhabit a wide range of habitats and prey on a diverse range of species.

The significance of play for dolphins is revealed by the persistence of play behavior. Dolphins of all ages play. Although young dolphins played more than older dolphins in our study, even the oldest dolphins played. Adult play is not unique to dolphins. Walters (1987) reported adult-adult play in great apes, but that most adult play in these species involved juveniles. Play has been observed in most contexts in which dolphins have been observed, despite the fact that play may increase the risk of predation or result in some form of injury (Fagen, 1993). Play is difficult to suppress in other species as well, particularly insofar as juveniles are concerned. For example, young fur seals play despite the risk of possible loss of life (Harcourt, 1991). Reductions in food availability may reduce the incidence of play, but rarely extinguish play altogether (Barrett, Dunbar, & Dunbar, 1992; Lee, 1984; Müller-Schwarze, Stagge & Müller-Schwarze, 1982; Sommer & Mendoza-Granados, 1995), suggesting that play has been evolutionarily maintained through the use of discretionary caloric expenditures (Caro, 1995).

Dolphin play may also provide insights into the processes involved in the creation and maintenance of animal culture. Culture has been defined as information or behavior that is acquired from members of one's species through social learning (Boyd & Richerson, 1996; Rendell & Whitehead, 2001). If so, then culture depends on both a conspecific that knows something that another member of the species does not and the ability and willingness of the less knowledgeable member to learn from the more knowledgeable one. Avital and Jablonka (2000) suggested that animal traditions must be actively constructed during ontogeny, a notion that emphasizes the role of other animals in the behavioral development of individual animals. Our observations of dolphin play support this hypothesis, and highlight the role of peers in cultural transmission and innovation.

Imitation is one form of social learning, and so may play an important role in the transmission of behaviors from one animal to another. Thus, determining who imitates whom in a given species will increase our understanding of the manner in which culture is transmitted in that species. Dolphin calves more quickly learned play behaviors that were already in the group repertoire if other calves were producing the behaviors. This suggests that calves are more salient models for other calves than are adults, including the calf's mother. In fact, dolphin calves seem to be more salient models for adult dolphins, given that adults proved more

likely to imitate novel play behaviors produced by calves than by other adults. Of course, this does not mean that calves never imitated adults. Calves did imitate some novel play behaviors produced by adults, and may also have imitated existing play behaviors that adults produced. Mothers were the most likely play partners during a calf's first two months of life, and so calves may have learned some play behaviors by observing and interacting with their mothers. In addition, calves may learn other forms of behavior from their mothers. Calves in Shark Bay, Australia, may learn to use sponges as they forage on the sea bottom by observing their mothers doing so (Krützen et al., 2005), just as infant chimpanzees may learn to crack nuts and fish for honey by watching adults (Boesch, 1991; Hirata & Celli, 2003).

The finding that the presence of other calves during play bouts facilitated mimicry is consistent with the notion that exploratory play enhances imitation of novel behavior (Miklosi, 1999). But why were calves more likely to mimic behaviors produced by other calves than those produced by adult dolphins, including their mother? Yando et al. (1978) suggested that similarity between model and imitator facilitated the imitator's mental representation of the observed behavior and so increased the chance that the observed behavior would be reproduced. Perhaps dolphin calves were more likely to mimic novel behaviors produced by other calves because the perceptual similarity between calves is greater than that between a calf and an adult (including the mother). However, this does not explain the influence of calves on the creative play produced by other calves. Nor does it explain observations of calves spontaneously imitating the behavior of humans (Kuczaj, Paulos, & Ramos, 2005), who are not physically very similar to dolphins and play either no or very small roles in dolphin social systems.

Perhaps calves were more likely to mimic other calves because mimicry increases the social cohesiveness of a calf group. Recently, van Baaren, Holland, Kawakami, and Knippenberg (2004) reported that adult humans who were imitated were more likely to be helpful and generous than were adults who had not been imitated. Moreover, this effect extended beyond the mimicker to other people, leading van Baaren et al. to conclude that imitation increases prosocial behavior in general. If this is the case for species other than humans, perhaps dolphin calves are predisposed to mimic other calves because such behavior helps to solidify positive social relationships within the peer group.

Although imitation may be an important aspect of cultural transmission, it is insufficient to explain cultural innovations. As Poirier and Fitton (2001) noted, studies of culture have typically focused on conformity, the ways in which known behaviors, information, and knowledge are transmitted among members of a culture. However, the innovators, what Poirier and Fitton called "agents of change," have been little studied. Clearly, the manner in which new behaviors appear and are added to a group's behavioral repertoire influences that group's culture. Our data suggest that peers provide models of possible behaviors and so play important roles in both the transmission of behaviors that are already part of the group's culture and in the creation of novel behaviors that are then gradually added to the group repertoire. In addition to being the most likely inventors of novel play behaviors and the most likely mimics of novel forms of play first produced by others, calves were also more likely than adults to produce novel play behaviors that other dolphins reproduced. Juvenile chimpanzees are more likely than adults to explore

novel food items (nuts), but are selective in their attention to peers attempting to crack nuts. Younger animals do not receive much attention, but same-age and older animals do (Biro, Inoue-Nakamura, Tonooka, Yamakoshi, Sousa, & Matsuzawa, 2003). These findings are reminiscent of Vygotsky's (1962, 1978) "zone of proximal development." Vygotsky hypothesized that human children benefited from social interactions with more competent individuals, the basic idea being that such social interactions pushed children to expand their capabilities. Thus, peers may have been more influential than other dolphins because they continually stimulated one another to either explore more complex forms of play and/or provided models of interesting play activities.

Given that an important part of an animal's enculturation consists of its interactions with other members of its species, interactions among peers may be significant for a number of reasons. They may help young animals learn their place in the social dynamics of the group, create bonds and alliances with other animals, and facilitate the acquisition of behaviors and abilities necessary for survival. The notion of animal culture is hotly debated in the current literature (e.g., see Rendell & Whitehead, 2001; Kuczaj, 2001; Tomasello, 1996), but it is difficult to imagine that animals do not learn from one another. Peer interactions during early development may be especially significant for cultural innovations. The innovations produced during the interactions of young animals may be important sources for the evolution of animal traditions, as well as the adaptations that may lead to more successful individuals and species (see Gottlieb, 2002, and Laland, Odling-Smee, & Feldman, 2000, for discussions of the roles of individual adaptation and culture in natural selection). It is possible that the ability to invent novel play behaviors and the ability to learn from the behaviors of others may be related to the creation and maintenance of animal traditions, and ultimately to the survival of species that engage in such behaviors. Additional research is needed to examine the relative roles of peers and adults in the acquisition of various forms of behaviors in a variety of species and contexts to determine the extent to which peers are agents of culture.

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Received April 5, 2005.

Revision received June 28, 2005.

Accepted July 1, 2005.