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How Selective is Social Learning in Dolphins?

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Social learning is an important aspect of dolphin social life and dolphin behavioral development. In addition to vocal social learning, dolphins discover behaviors for foraging, play, and social interactions by observing other members of their social group. But dolphins neither indiscriminately observe nor mindlessly mimic other dolphins. To the contrary, dolphin calves are quite selective in their choices of who to observe and/or imitate. Calves are most likely to learn foraging behaviors from their mothers, but they are more likely to watch and reproduce the play behaviors of other calves than the play behaviors of adult dolphins (including their mothers). But not all calves are equally likely to be good models. Instead, calves are more likely to observe and mimic the behaviors of other calves that are producing either novel behaviors or more complex forms of behaviors that the observing calf already knows. As a result, there is a general tendency for calves to watch and learn from calves that are older than they are. But differences in age are only part of the story. In fact, dolphin personality may be more important than dolphin age in determining the efficacy of a model.

Although the human capacity for observational learning has been well documented (e.g., Bandura, 1997; Meltzoff & Prinz, 2002; Piaget, 1962), the role of such learning in the ontogeny of animal behavior is much less clear. However, the possibility that non-human animals (referred to as animals from here forward) acquire behaviors and information about their environment from watching others has intrigued scholars for approximately 150 years. For example, many pioneering scholars with interests in the comparative study of behavioral development believed that social learning was an important aspect of the ontogeny of behavior for humans and animals, but that the social learning of non-humans reflected primitive mental abilities compared to the social learning and mental capacities of humans (Baldwin, 1895; Darwin, 1871; Morgan, 1900; Romanes, 1883; Thorndike, 1898; Wallace, 1870; Washburn, 1936). The notion that human social learning and animal social learning are qualitatively distinct has survived the intervening years, although the exact nature of these differences remains a matter of dispute (Box & Gibson, 1999; Herman, 2006; Heyes, 1993; Kuczaj, Paulos, & Ramos, 2005; Laland & Galef, 2009; Snowden & Hausberger, 1997; Tomasello, 1999).

Regardless of these disputes, it is clear that animals and humans can learn via observation in a number of ways (Tomasello, 1999). Observation can lead to increased interest in locations (local enhancement), objects (stimulus enhancement), or outcomes (goal enhancement). In each of these cases,

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observational learning facilitates acquisition of information about one's environment. It can also provide valuable insights about behavior. Imitation is a form of observational learning that occurs when individuals learn about behavior from observing others (Heyes, 1993; Tomasello, 1999). Both types of social learning are obviously beneficial, although it seems that acquiring behavior via observation is rarer than is learning about one's environment by observing others.

Regardless of whether one is acquiring information about one's environment or about possible behaviors, observational learning facilitates the transmission of information from one individual to another (Galef, 2003; Kuczaj et al., 2005; Kuczaj & Yeater, 2006). The spread of adaptive novel behaviors in a group may be hastened by observational learning, and consequently observational learning may increase an individual's chances of surviving and reproducing. Kuczaj and Yeater (2006) suggested that observational learning, behavioral flexibility, and culture were intertwined. Although the human capacities for flexibility and observational learning have contributed to a wide array of cultures, the extent to which culture exists in animal societies remains controversial (Kuczaj, 2001; Laland & Galef, 2009; Rendell & Whitehead, 2001). Nonetheless, there is general agreement that some form of social learning is necessary in order for any culture to evolve and thrive (Boyd & Richerson, 1996, 2000; Laland & Galef, 2009; Rendell & Whitehead, 2001).

In the remainder of this paper, we consider aspects of dolphin observational learning with a focus on the selective nature of dolphin social learning. As we shall demonstrate, it is not the case that dolphins indiscriminately observe or mindlessly imitate the behavior of other dolphins. To the contrary, dolphin calves are quite selective in their choices of who to observe and/or imitate. Their decisions about who and what to imitate are influenced by the context, the novelty of the behavior, and the personalities of both the model and the observer.

How Selective is Vocal Learning in Dolphins?

Vocal learning involves the acquisition of acoustic forms as the result of experience (Janik & Slater, 2000). The necessary experience is often social in nature, and in such cases can be considered a form of social learning. Social vocal learning is relatively rare in non-human mammalian species, but appears to play a major role in the acquisition of each individual dolphin's acoustic repertoire (Janik & Slater, 2000). Of course, vocal learning need not involve selective social learning. Hence, we will limit our consideration of vocal learning in dolphins (and other cetaceans) to those cases in which selective social learning is involved.

Killer whales (*Orcinus orca*), the largest dolphin species, have vocal dialects (i.e., Ford, 1991; Deecke, Ford, & Spong, 2000). Stable groups of resident killer whales possess group-specific call repertoires that are acoustically distinct from the repertoires of other groups (Ford, 1991). Vocal matching among killer whales typically occurs within members of a matriline (Miller & Bain, 2000; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Despite the fact that killer whale calves are exposed to the calls of their group's dialect and the calls of other groups, they appear to selectively attend to and learn the calls of their matrilineal group. Although it seems clear that killer whale calves learn the calls of their dialect from

maternally related individuals, it is not clear which members of their pod contribute the most to their selection of their vocal repertoire. However, Bowles, Young, and Asper (1988) studied the ontogeny of a female killer whale calf's vocal calls in captivity during the first year of life, and found that the calf learned most of her calls from her mother despite the fact that another adult female was housed with them. This female produced different calls than the mother and also called more frequently than did the mother. Nonetheless, the calf selectively attended to and reproduced its mother's calls. Although these results suggest that killer whale calves may learn much of their acoustic repertoire from their mothers, the Bowles et al. (1988) study does not distinguish the effects of vocal learning and maturational processes (see Janik & Slater 1997; Yurk et al., 2002). In addition, the extent to which mothers contribute to the vocal repertoire of wild killer whale calves remains to be determined.

The selective learning of group calls by killer whale calves does not reflect a universal tendency among killer whales to avoid the use of calls produced by other groups of killer whales. Matching does occur during vocal exchanges between individual members of distinct matrilineal groups (Deecke et al., 2000; Miller, Shapiro, Tyack, & Solow, 2004). In fact, Filatova, Burdin, and Hoyt (2010) reported that killer whales learn calls from other adults through horizontal transmission across pods. Thus, the selective acoustic learning by killer whale calves reflects a dialect repertoire acquisition predisposition rather than a general tendency of whales to ignore the sounds produced by members of other groups. In other words, killer whales can selectively learn call types through vertical transmission of information (from mother to offspring) and selectively learn calls from other adults. At present, it is not clear exactly what determines which calls an individual whale selects to reproduce, particularly in cases of horizontal transmission.

Additional evidence for selective social learning in the acquisition of dolphin communicative acoustic signals comes from the literature on dolphin signature whistles. Caldwell and Caldwell (1965) first discovered that individual dolphins produced distinctive vocal signals, which they termed signature whistles. Such whistles appear to play a role in individual recognition and may function as contact calls (Cook, Sayigh, Blum, & Wells, 2004; Harley, 2008; Sayigh, Esch, Wells, & Janik, 2007; Sayigh, Tyack, Wells, Solow, Scott, & Irvine, 1999; Tyack, 2000; Watwood, Owen, Tyack, & Wells, 2005). McCowan and Reiss (2001) argued against the notion of signature whistles per se, but concluded that "individual variability in the production of a shared contact call, as reported for other taxa, probably accounts for individual recognition in dolphins" (p. 1151). Despite disagreements concerning the nature of signature whistles, it is clear that dolphin calves learn signature whistles via social learning. It is possible that the mother is a significant source of information regarding signature whistles and that calves develop their own signature whistles through whistle exchanges with their mothers (Sayigh, Tyack, Wells, & Scott, 1990). However, the extent to which calves mimic their mothers' signature whistle depends at least in part on the calf's gender. Male calves tend to produce whistles that are similar to their mothers, but female calves are more likely to produce whistles that are quite different than their mothers (Sayigh et al., 1990; Sayigh, Tyack, Wells, Scott, & Irvine, 1995).

Dolphin calves spend the first three to six years in close proximity to their mother, and so there are ample opportunities for calves to learn the signals their mothers produce (Wells, Scott, & Irvine, 1987). The differential selective learning of mothers' signals by males and females may reflect each gender's roles in its natal group. Females tend to stay with their matrilineal group, but males disperse from their natal group once they reach sexual maturity (Wells et al., 1987). As a result, females may need to develop distinctive signature whistles in order to distinguish themselves from their mothers given that they may remain in relatively close proximity to their mothers throughout their lives. The possibility of selective social learning in this process was raised by Fripp et al. (2005), who suggested that female calves may select the models for their signature whistles from dolphins with whom they spend only a small amount of time. Such selectivity would serve to make the learner's own whistles more distinguishable from individuals with which they more commonly associate. Sayigh et al. (1990, 1995) suggested that males selectively learn a whistle similar to their mother's to help prevent inbreeding, and/or to maintain contact with kin once they have dispersed from the natal group. Although the precise reasons for female and male calves' differential use of the mother's signature whistle is unclear, selective social learning is evident from the fact that females usually do not adopt their mother's whistle, while males tend to copy their mother's whistle, a clear and perhaps unique form of gender specific selective social learning in mammalian acoustic development.

Selective Behavioral Learning by Dolphins

In addition to vocal social learning, dolphins discover behaviors used for foraging, play, and social interactions by observing other members of their social group. The dolphin capacity for social learning is widely recognized (Kuczaj, Paulos, & Ramos, 2005; Kuczaj & Yeater, 2006; Marino et al., 2007; Yeater & Kuczaj, 2010). In fact, social learning appears to be an important aspect of dolphin social life and dolphin behavioral development (Kuczaj & Yeater, 2006; Yeater & Kuczaj, 2010). Dolphins can imitate their own behavior (Mercado, Murray, Uyeyama, Pack, & Herman, 1998; Mercado, Uyeyama, Pack, & Herman, 1999) as well as that of other dolphins (Bauer & Johnson, 1994; Herman, Morrel-Samuels, & Brown, 1989; Xitco, 1988) and even other species (see Kuczaj & Yeater, 2006 and Yeater & Kuczaj, 2010 for reviews of the literature on dolphin imitation).

For example, Taylor and Saayman (1973) observed a captive bottlenose dolphin calf attempting to reproduce the smoke that was exhaled from a human's mouth. After watching the human smoke a cigarette, the calf swam away, nursed from its mother, returned to the window, and released the milk from its mouth, the result being a smoke-like cloud of milk in the water. Another case from Taylor and Saayman (1973) illustrates the creativity that dolphins can employ in their attempts to reproduce what they have observed:

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. (p. 290)

More recent observations have demonstrated that dolphin calves frequently learn via observation, sometimes acquiring new behaviors in the process (Kuczaj et al., 2005; Kuczaj & Yeater, 2006). Kuczaj and Yeater (2006) provided the following description of observational learning they had witnessed:

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. (p. 417)

Other examples demonstrate that social learning facilitates the acquisition of new behaviors by members of a dolphin social group. Kuczaj et al. (2005) observed a dolphin calf playing with a football by repeatedly releasing and retrieving the football in a submerged box under a dock. Other dolphins watched the calf manipulate the football in this novel manner, and within a few days another calf and three adults were playing the same game with the football. Other examples of novel behaviors spreading among dolphin populations include seaweed carrying and balancing on the edge of a tank (Pryor, 1975).

The dolphin capacity for selective social learning may rest in part on their ability to spontaneously synchronize their behaviors (Bauer & Harley, 2001). Support for the notion that synchrony involves imitation comes from a study of elicited synchronous behaviors (Herman, 2002). Two dolphins were asked to perform a number of synchronous behaviors. The dolphins proved adept at doing so, but video analysis revealed that one dolphin typically led the other, suggesting that the trailing dolphin was imitating the behavior of the lead dolphin. Synchronous behavior occurs early in dolphin mother-calf interactions, and so calves may be predisposed to pay attention to the behavior of their mothers, a predisposition that may set the stage for later social learning. However, it is also possible that the ability to synchronize behavior rests on the capacity for social learning. Further research is needed to better determine the ontogenetic relationship of synchrony and social learning.

Selective Social Learning in the Acquisition of Foraging and Play Behaviors

In the wild, some of the best evidence for selective social learning comes from dolphin calves learning foraging strategies by observing their mothers (Bender, Herzing, & Bjorklund, 2008; Boran & Heimlich, 1999; Sargeant, Mann, Berggren, & Krützen, 2005; Sargeant & Mann, 2009). Learning from observing the mother seems to be the most common way in which dolphin calves develop foraging techniques (Bender et al., 2008; Guinet & Bouvier, 1995), although opportunities for learning from other adults also occur (Guinet & Bouvier, 1995; Mann, Sargeant, & Minor, 2007). Evidence for selective social learning from the mother has been found for many foraging strategies, including beach hunting, sponge carrying, mill foraging, and rooster-tail foraging (Bender et al., 2008; Guinet & Bouvier, 1995; Sargeant & Mann, 2009; Sargeant et al., 2005). For example, a small group of female bottlenose dolphins in Shark Bay, Australia use sponges to protect their rostrums (noses) while foraging on the ocean floor (Smolker, Richards, Connor, Mann, & Berggren, 1997), a behavior that seems to be passed on from mothers to daughters, although the precise form of social learning that is involved is currently unknown (Krützen et al., 2005; Sargeant & Mann, 2009). The social learning involved in the transmission of sponge carrying foraging is selective in two senses: (1) Calves learn this behavior from their mothers, and (2) female calves are more likely to acquire this behavior than are male calves. At this time, it is unknown whether mothers do not demonstrate this technique to their sons or if the sons elect not to mimic the mothers' sponging behaviors. Nor is it clear why this gender difference exists.

Bender et al. (2009) reported that Atlantic spotted dolphin mothers (*Stenella frontalis*) engaged in behaviors that seem intended to attract and maintain their calves' attention to the foraging techniques being demonstrated by the mother. The mothers extended their pursuit of fish and used more referential pointing movements (see Xitco, Gory, & Kuczaj, 2001, 2004, for discussions of dolphin pointing behavior) during these teaching bouts than in regular fish pursuits, such behaviors increasing and directing the calves' opportunities to observe the mother's behavior. In addition, when mothers were foraging with their attentive calves, the mothers sometimes let the prey escape, after which the mother either recaptured the fish or allowed the calf to chase the prey. Although the mothers altered their behavior during these teaching bouts, the prey was always consumed at the end. The mothers, then, seemed to have considerable control over the prey, which was used to capture their calves' interest, the result being a rich opportunity for the calves to learn foraging behaviors by carefully watching the mother and sometimes even practicing foraging behaviors themselves.

Killer whales in the Crozet Islands and off Punta Norte, Argentina capture seal pups by intentionally stranding themselves on 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 another related adult female. Therefore, this type of learning is

unique in that calves selectively attended to the individual that was most successful at using intentional stranding to capture seal pups. This finding fits well with other research that has shown that dolphins, particularly dolphin calves, are quite selective in terms of who and what they elect to imitate (Kuczaj, Makecha, Trone, Paulos, & Ramos., 2006; Kuczaj & Yeater, 2006; Yeater & Kuczaj, 2010). Not all models are treated equally by observing dolphins, and their decisions about whom and what to imitate is another indication of the selectivity of their social learning.

Dolphin calves are more likely to imitate the play behaviors of other calves than they are to imitate the play behaviors of adults, including their mothers (Kuczaj et al., 2006). However, some calves are more likely to be imitated than others. In general, young dolphins are more likely to imitate the play of older (and more competent) peers than younger less competent peers. But differences in age are only part of the story. In fact, personality may be more important than age.

Animal Personality

Personality has been studied in a variety of species (see Gosling 2001), including dolphins (Highfill & Kuczaj, 2007). A number of personality characteristics have been suggested to exist in animals, including playfulness, agreeableness, and boldness. Of these, the timid-bold continuum has garnered the most attention from animal personality researchers (Wilson, Clarke, Coleman, & Dearstyne, 1994). The timid-bold personality dimension may directly influence selective social learning in that bold individuals may be more likely to be watched by others and consequently may also be more likely to be chosen as models. This possibility is given additional support by research demonstrating that where an animal falls on the timid/bold dimension may impact its ability to learn. For example, Svartberg (2002) found that bold dogs (*Canis familiaris*) outperformed timid dogs on tasks such as searching for a hidden person and protecting the handler. Similarly, bold European starlings (*Sturnus vulgaris*) were quickest to feed in a novel environment and also required fewer trials to learn a foraging task (Boogert, Reader, & Laland, 2006). Bold black-capped chickadees (*Poecile atricapillus*) more readily entered a novel environment and also more quickly learned an acoustic discrimination task (Guillette, Reddon, Hurd, & Sturdy, 2009). If bold animals are more likely to learn new behaviors than are timid animals, evolutionary pressures may have selected for a predisposition to attend to the behaviors of bold individuals and to selectively reproduce the modeled behavior, depending on the consequences the behavior yielded for the model.

In addition to the link between boldness/timidness and individual learning, there is also evidence for a relationship between neophobia (a fear of new things or experiences), innovation, and social learning. Bouchard, Goodyer, and Lefebvre (2007) assessed the amount of time it took individual adult pigeons (*Columba livia*) to feed near a novel object. The pigeons' innovative problem-solving abilities were then examined using complex feeding problems. Finally, pigeons were tested on their ability to learn how to use a feeding device after observing a trained pigeon demonstrate the correct solution. Pigeon performance on the innovative problem solving task and the social learning task was strongly correlated. More importantly for this discussion, bolder pigeons were more

innovative and learned via observation more quickly than did the more timid pigeons. Although the above examples suggest a relationship between bold personalities and learning abilities in pigeons, additional research with different species and different learning tasks is sorely needed.

Timid/Bold Continuum in Dolphins and their Selective Social Learning

Dolphins possess clearly defined personality types that are stable through time, and one of the dimensions on which individual dolphin personalities differ is the timid/bold continuum (Highfill & Kuczaj, 2007). Dolphins exhibit individual personalities from an early age, and the more curious and bold animals are the ones that are most likely to be observed and mimicked (Kuczaj et al., 2006). For example, when a novel object is encountered, bolder calves and juveniles are the first to examine the object, and it is not unusual to see the more cautious calves hovering a short distance behind the bolder animals. The cautious dolphins appear to be looking over the bolder dolphins' "shoulders," and are careful to keep the bold calf between themselves and the novel object. As the bold animals begin to more actively explore and even manipulate the novel object, the cautious animals move away but keep a close watch on the interaction between the bold models and the object. Only after the cautious animals have witnessed the bold animals' successful manipulations of the object do they dare approach the object and attempt to replicate the model's behaviors, a process which may take days in the case of extremely novel objects such as a bubble ring producing machine or an artificial human swim leg.

Two of our recent observations serve to illustrate the effects of boldness/timidness on object exploration and social learning. In one case, we exposed a group of 24 dolphins to a machine that produced underwater bubble rings. None of the dolphins had seen the machine before and none of the dolphins had been observed blowing bubble rings before. Thus, both the rings and the machine were novel to the dolphins. As we expected, bold dolphins were most likely to visually examine the machine and to manipulate the bubble rings it produced (see Figure 1). As shown in Figures 2 and 3, a bold dolphin was often accompanied by a more timid dolphin that lurked behind or above its bold counterpart. In fact, no timid dolphin examined the bubble machine during the first two days it was in the water unless the timid dolphin was shadowing a bold dolphin. However, on the third day, two of the timid dolphins began to approach the machine on their own. In each case, the dolphins' initial exploration of the machine mirrored that of its earlier bold partner.

Our other example involves an artificial swim leg used by an amputee who was assisting with underwater data collection. Although superficially similar to a normal human leg, the artificial leg proved irresistible to the dolphins. They echolocated on it extensively, and even nudged and mouthed it on several occasions. Once again, the bold dolphins were the ones to initially actively explore the novel leg, oftentimes with other less bold dolphins observing the bold dolphins' interaction with the limb, which gradually transitioned from echolocation on the leg to mouthing of the foot of the limb. By the fifth day, the more timid

dolphins were also touching the foot of the leg, typically by gently mouthing it as their more adventuresome peers had done days earlier.



Figure 1. A bold dolphin sticks its rostrum through a bubble ring.



Figure 2. A bold dolphin closely examines a bubble ring while a more timid dolphin looks on.



Figure 3. One of the bolder dolphins breaks a bubble ring while another dolphin observes.

What is the Function of Selective Social Learning?

Dolphin calves are selective in their choices of who to observe and imitate. There are a variety of factors that influence whether or not a human imitates another human's behavior (Bandura, 1986), and similar factors affect a dolphin's willingness to mimic the behavior of another dolphin (Kuczaj & Yeater, 2006). These factors include the behavioral context, the novelty of the modeled behavior, the ages of the observer and the model, and the personalities of the observer and the model.

Dolphin calves are most likely to learn foraging behaviors from their mothers, and also appear to learn at least part of their acoustic signal repertoire as a function of the sounds their mothers produce. Thus, calves appear to pay considerable attention to their mothers in both communicative and foraging contexts. However, to summarize findings by Kuczaj et al. (2005), calves are more likely to watch and imitate the play behaviors of other calves than they are to imitate the play behaviors of adult dolphins (including their mothers). But not all calves are equally likely to be good models. Instead, calves are more likely to observe and mimic the behaviors of other calves that are producing either novel behaviors or more complex forms of behaviors that the observing calf already knows. As a result, there is a general tendency for calves to watch and learn from calves that are older than they are.

But relative age of the model and the observer is only part of the story. Dolphins exhibit distinct individual personalities from an early age, and the more curious and bold animals are the ones that are most likely to be observed and

imitated by other dolphins. As discussed above, when a novel object is encountered, the more bold calves and juveniles are the first to examine the object, oftentimes with more cautious calves hovering behind the bolder animals. Therefore, personality may play a more important role than age in social learning insofar as determining which individuals are chosen as models. The cautious dolphins appear to be looking over the bolder dolphins' "shoulders," and are careful to keep the bold calf between themselves and the novel object. As the bold animals begin to more actively explore and even manipulate the novel object, the cautious animals move away but keep a close watch on the interaction between the bold models and the object. Only after the cautious animals have witnessed the bold animals' successful manipulations of the object do they dare approach the object and attempt to replicate the model's behaviors, a process which may take days in the case of extremely novel objects such as a bubble ring producing machine or an artificial human swim leg.

There is one factor that influences dolphins' selective social learning regardless of general behavioral context, age, and personality. In general, dolphins are more likely to observe and reproduce novel behaviors than behaviors they already know. Innovation by an individual is necessary in order to add new behaviors to a group's behavioral repertoire, even though it is not the case that all innovations are adopted by all group members. Over one hundred years ago, Morgan (1900) suggested that model behaviors observers found interesting would be imitated more often than would mundane behaviors, and it seems reasonable to assume that innovative behaviors would be more interesting to an observer than would familiar ones. Support for this idea was found by Kuczaj et al. (2005). In their study, dolphin calves were more likely than adults to produce innovative play behaviors and that these novel play behaviors were more likely to be reproduced by other calves than were familiar play behaviors.

We suspect that personality is a contributing factor to behavioral innovations. Bold dolphins are more curious and so more likely to investigate and interact with novel objects. They are also more likely to modify their own behavior to keep it interesting, a phenomena we have observed quite often in dolphin play. For example, one of the bolder killer whales observed by Kuczaj and Walker (2006) modified its gull catching behavior in order to make successful apprehension of a gull more difficult. Dolphins make their play more difficult in order to keep the play activity interesting, and in so doing create the sorts of moderately discrepant events, when assimilating to a new situation, that facilitate cognitive growth and behavioral flexibility (Kuczaj & Walker, 2006). Bold animals are more likely to create their own challenging scenarios than are timid animals, and so it appears that self-handicapping and social learning are both influenced by dolphin personality.

Bold individuals, then, are significant contributors to a group's behavioral repertoire in a number of ways. They provide interesting models for others to observe (Kuczaj et al., 2005; Morgan, 1900). These bold models provide valuable information about what is possible and what is not – some behaviors initiated by bold individuals may result in injury or death, and so even failures can provide life-saving information to others. We concur with Morgan's (1900) suggestion that the absence of interesting models may result in reduced curiosity and innovation in

a group of animals, and so bold animals may be the lifeblood of cultural change for dolphins and other animals.

Bold animals may also be more likely to be observed and mimicked because they possess social status that timid animals do not (see Bandura, 1986, for a discussion of the relationship of status and imitation in humans). Bold animals tend to have a higher social standing; therefore, timid animals may reproduce the behavior of bold animals in order to gain social acceptance. Imitation increases pro-social behavior (behaviors which benefit others, such as helping or generosity) among adult humans (van Baaren, Holland, Kawakami, & van Knippenberg, 2004), and so imitating a bold peer may result in that peer increasing its pro-social behavior, an obvious benefit to timid animals. Human adults who feel excluded from a group are more likely to mimic the behavior of a member of the group (Lakin, Chartrand, & Arkin, 2008), and it seems plausible that timid dolphins mimic the behavior of bolder animals at least in part to improve their status within the group. The social consequences of imitating or being imitated are likely to be powerful forces that influence selective social learning, and so are worthy of much needed additional investigation.

To sum up, social learning in dolphins is selective (Kuczaj et al., 2005; Kuczaj & Yeater, 2006; Yeater & Kuczaj, 2010), a phenomenon that is influenced by behavioral context, novelty of the behavior, significance of the model, and personality. We suspect that selective social learning also explains at least in part the discrepancy between spontaneous imitation and elicited imitation. Dolphins are much more adept at spontaneous imitation than elicited imitation (Kuczaj & Yeater, 2006), and the opportunity to select both the model and the behaviors to be reproduced in spontaneous imitation seems to enhance social learning in ways that elicited imitation tasks cannot.

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