

Cetacean Innovation

Eric M. Patterson¹ and Janet Mann^{1,2}

¹Department of Biology, Georgetown University, Washington DC, USA

²Department of Psychology, Georgetown University, Washington DC, USA

A cloud of cigarette smoke was once deliberately released against the glass as Dolly was looking in through the viewing port. The observer was astonished when the animal immediately swam off to its mother, returned and released a mouthful of milk which engulfed her head, giving much the same effect as had the cigarette smoke. (Tayler & Saayman, 1973)

Commentary on Chapter 4: Proto-c Creativity?

Vlad Petre Glăveanu

Aalborg University, Department of Communication and Psychology, Aalborg,
Denmark

INTRODUCTION

Dolly's "milk smoking" is just one of many fascinating behaviors Tayler and Saayman observed in Indian Ocean bottlenose dolphins (*Tursiops aduncus*) at the Port Elizabeth Oceanarium in South Africa in the 1970s. Not only did Dolly parade her impressive imitation abilities and potential analogous reasoning, she gave us a peek into her creative mind. But of what use would such creative behavior be in the wild? Milk smoking would certainly be maladaptive for a young, hungry calf, but could similar creative abilities be beneficial, say, for exploiting new

resources or obtaining mates? Only recently have such questions been the subject of empirical work in ethology.

To date, most data on animal innovation come from primates and birds. After scouring the literature for anecdotal observations of novel behavior and carefully controlling for confounding factors (e.g., phylogeny, research effort, observation biases, etc.), Laland, Lefebvre, Reader, Sol, and colleagues have provided some of the most intriguing data on animal creativity and innovation (Lefebvre, Reader, & Sol, 2013; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader & Laland, 2001). Although these studies are impressive, they are taxonomically limited. As such, we need to expand our efforts to include additional taxa, but given the infancy of the study of animal innovation, where does one start? To address this question, we briefly consider the conditions thought to promote innovative and creative behavior across taxa, which can be divided into intrinsic factors (characteristics of the individual itself), and extrinsic factors (external social and ecological conditions).

First, for an individual to be creative and capable of innovation it must be behaviorally plastic so that new or modified behaviors can be introduced into its repertoire (Reader & Laland, 2003). Closely related is that an individual must have the ability to learn (Reader & Laland, 2003). Yet, learning is likely ubiquitous among animals and even argued for plants (Gagliano, Renton, Depczynski, & Mancuso, 2014), so learning itself adds little to our understanding of creative and innovative behavior. More important is an individual's capacity for social learning, which is required for behaviors to spread and persist in a population, and therefore be of evolutionary interest. Additionally, given the central role of novel behavior in both innovation and creativity, an individual with neophilic tendencies may be predisposed to innovate and be creative (Greenberg, 2003; Reader, 2003).

Second, an individual's proclivity to innovate and be creative will depend on both its social and ecological circumstances. For example, social conditions that provide free time are thought to favor innovation and creativity (Kummer & Goodall, 1985). In particular, a period of extended maternal care in which young are relatively free from energetic constraints may be important for allowing individuals to learn and explore their environment with minimal costs. Social or group living may also foster innovation and creativity. Not only do social interactions create opportunities for social learning, they expose individuals to behavioral variation that can be learned and modified to produce novel behavior (Lee, 2003; Reader & Laland, 2002). Furthermore, group living generally reduces predation risk and vigilance (Alexander, 1974) and thus, allows for otherwise costly behaviors and tendencies like exploration, play, boldness, and openness (De Oliveira, Ruiz-Miranda,

Kleiman, & Beck, 2003; Huang, Sieving, & Mary, 2011; Moller & Garamszegi, 2012; Panksepp, 1998). Certain ecological conditions, such as stable environments with abundant resources, may also afford individuals discretionary time and reduce the costs of exploratory behavior (Reader & MacDonald, 2003). On the other hand, highly variable environments present individuals with new challenges that may require innovative and creative solutions (i.e., “necessity is the mother of invention,” Sol, 2003), while learning, an intrinsic requirement noted above, is favored in moderately changing environments (Stephens, 1991). Thus, at least some between generation ecological variability in a species’ evolutionary history is vital, but beyond this, both ecological stability and variability within generation contribute to the expression of innovative and creative behavior.

Many of these intrinsic and extrinsic factors commonly associated with innovation and creativity are characteristic of cetacea, especially odontocetes. First, cetaceans are extraordinarily plastic in their behavior as exhibited by the great diversity of foraging tactics within and between populations (e.g., *Tursiops* spp., Connor, Wells, Mann, & Read, 2000; *Megaptera novaeangliae*, Clapham, 2000). They are also generally considered curious, inquisitive animals (Birtles & Mangott, 2013). In captivity, odontocetes demonstrate a high degree of neophilia (Defran & Pryor, 1980; Nakahara & Takemura, 1997; Terry, 1986), and in the wild, both odontocetes and mysticetes manipulate almost any new object they come across (Paulos, Trone, & Kuczaj, 2010; Würsig, 2008). Odontocetes also display impressive learning abilities, in particular social learning (e.g., Sargeant & Mann, 2009), with bottlenose dolphins demonstrating some of the most impressive imitation abilities of any nonhuman animal (Herman, 2002). Cetaceans also have an extended period of maternal dependency (Whitehead & Mann, 2000), with calves engaging in extensive social play and exploration (e.g., Gibson & Mann, 2008; Mann & Watson-Capps, 2005). Female cetacea give birth to a single (except in rare cases of twins, Olesiuk, Bigg, & Ellis, 1990), large, precocial calf, often born into a highly social environment (Chivers, 2009). Odontocete calves are particularly slow growing and generally nurse for over a year (Oftedal, 1997), with some delphinids nursing for 9 years or more (Kasuya & Marsh, 1984; Mann, Connor, Barre, & Heithaus, 2000). Furthermore, because cetaceans can store energy in their blubber, they can capitalize on ephemeral abundant resources, which may reduce foraging demands and allow for exploratory behavior. Finally, as top predators often living in groups, cetaceans may be less vigilant or “fearful” than species with high predation risk, a state which may otherwise inhibit exploration. Thus, these social, behaviorally plastic, neophilic, mammalian predators not only exhibit all the conditions thought to promote innovative and creative behavior, if

studied in greater detail, they may prove to be one of the more innovative and creative taxa, a subject this chapter attempts to examine in detail.

Although some authors note the apparent innovative abilities of cetaceans (e.g., Kaufman, Butt, Kaufman, & Colbert-White, 2011; Lee, 2003; Sol, 2003), direct literature on the subject is sparse. This is in part due to the logistical difficulties of studying at sea, but even existing accounts of innovative and creative cetacean behavior offer only basic descriptions and rarely consider such observations in a comparative context. In this chapter, we hope to address this gap by reviewing possible cases of innovative and creative behaviors in both captive and wild cetaceans. However, before we do, we must operationalize the terms creativity and innovation.

Defining creativity and innovation is no simple task even though both concepts have intuitive meanings. The subject has been covered in great depth by others (e.g., Kaufman & Kaufman, 2004; Plucker, Beghetto, & Dow, 2004; Ramsey, Bastian, & van Schaik, 2007; Reader & Laland, 2003; Simonton, 2003), so we will only briefly touch on it here. While some treat creativity and innovation as if they are synonymous, we agree with Bateson and Martin (2013) that the two overlap but are not interchangeable. For us, creativity refers more to the cognitive processes that *directly* generate novelty, whereas innovation involves implementing novelty in a useful way. Not all innovations arise from creativity, nor does all creativity result in innovation. To illustrate the first point, consider the classic animal innovation of milk bottle opening by European blue tits (*Cyanistes caeruleus*) (Fisher & Hinde, 1949). Perhaps the first bird to open a milk bottle did so accidentally, by pecking at an insect crawling on the bottle's foil cap. After fishing out the insect, the bird would immediately be rewarded with milk and, consequently, might learn to open bottles solely for milk. In this scenario, learning would be involved, but the initial milk reward would just be a fortuitous *by-product* of cognition related to insect foraging, and so this innovation would not involve creativity. Our second point, that creative acts do not always lead to innovations, is more obvious since probably all human artworks involve creativity, but most are not considered innovations.

In this chapter we apply the term innovation to all novel or modified, functional behaviors. However, we only consider the modification of a behavior innovative if the modified component has some functional outcome unique from that of the original behavior. We use the term creative when it seems likely that a novel behavior is the *direct* product, rather than the by-product, of some underlying cognitive process, regardless of what that process is and whether or not the behavior has some function. Unfortunately, in animal studies usually only the

product, novel behavior, rather than the process that creates it is known. Because of this gap, we describe most behaviors simply as innovations and only discuss a few in the context of creativity. In our coverage of cetaceans, we rely on researcher reports of species-atypical novel, unique, or unusual behaviors that might be innovative or creative, which is similar to the approach that has been used for birds and primates (Lefebvre et al., 1997; Reader & Laland, 2001).

In the following sections, we will (i) provide examples of innovative and creative behavior from captivity, (ii) examine possible cases of such behavior in wild cetaceans, (iii) discuss what both of these datasets tell us about cetaceans' creative and innovative abilities, and finally (iv) contrast cetacean data with other taxa to provide comparative insight on the evolution of animal creativity and innovation.

TALES FROM THE TANK

Observations from captivity provide some of the best examples of innovative and creative behavior in cetaceans. With no predators, foraging demands, nor obvious costs, captive animals have ample time to spare and their captive environments present new, albeit artificial, social, and ecological challenges (Kummer & Goodall, 1985). Furthermore, most aquaria have trainers that encourage new behaviors. While many novel behaviors from aquaria are unlikely to be of use in the wild (e.g., milk smoking), examining a species' tendency to innovate and be creative in captivity can be informative, especially for difficult to study taxa such as cetaceans.

The first published record of a captive cetacean dates back to the early 1860s (Wyman, 1863), although some reports go as far back as the first century AD (Corkeron, 2009). To date, some 35 species have been held in captivity, just over a third of the 92 currently recognized (Defran & Pryor, 1980; Perrin, 2014). This captive sample is extremely odontocete-biased, with only two species of mysticetes, gray (*Eschrichtius robustus*) and minke whales (*Balaenoptera acutorostrata*), represented. Moreover, most are delphinids, particularly bottlenose dolphins (*Tursiops* spp. [*truncatus* and *aduncus* species]), which here we will discuss as one taxonomic group). In fact, of the current 576 reported captive cetaceans in the United States, around 94% are delphinids (83% from genus *Tursiops*), with only a few representatives of the phocoenidae and monodontidae families (National Marine Fisheries Service Office of Protected Resources, 2014). Nonetheless, in the taxa represented, examples of novel or modified behavior are plentiful and

widespread, the most impressive of which we review below. To help illustrate the breadth of these behaviors, we group them by their apparent function (play, vocal communication, foraging).

Play

Play, or play-like behavior, is notoriously difficult to study, but has been of great interest to animal behaviorists for well over a century (Bekoff & Byers, 1998; Groos, Baldwin, & Baldwin, 1898). Generally speaking, play behavior consists of actions that appear to have no immediate purpose other than their own enjoyment (Bekoff & Byers, 1981). However, play is often thought to be a form of practice and important for normal development (Bekoff & Byers, 1981), so here we consider it functional. In what is almost certainly the first published report on the behavior of a captive cetacean, Wyman (1863) describes the “playful disposition” of a captive male beluga (*Delphinapterus leucas*) who used to amuse himself by tossing stones, or, on occasion, capturing fishes in his tank only to later release them unharmed. Observations similar to this are common, with captive odontocetes voluntarily manipulating and playing with a variety of natural and unnatural objects (Paulos et al., 2010), in addition to any items they are deliberately trained to manipulate. In aquaria, odontocetes clearly regularly interact and play with novel objects, but are these behaviors innovative and do they tell us anything about cetacean creativity?

We can attempt to answer this by examining a few play behaviors in more detail. In noting the behavior of bottlenose dolphins at Marineland of Florida, Tavalga (1966) describes two calves playing a rather unique game of fetch. One calf would bring a pelican feather (or sometimes a handkerchief) to an intake jet in the facility and allow the strong current to carry the feather up toward the surface. The other calf, stationed along the feathers path, would then catch the feather, after which the two would switch positions and repeat the process all over. At the same facility, a short-finned pilot whale (*Globicephala macro-rhynchus*) invented a game almost the exact opposite in nature. Kritzler (1952) describes how the whale would remove a piece of flotsam from the drain near the center of the tank, swim a short distance away, release the item, and then follow it slowly as it was sucked back in by the vortex. Meanwhile, at Marineland of the Pacific, a male bottlenose dolphin named Frankie was also observed playing the feather jet game, although only by himself. Here the behavior eventually spread to other individuals and sometimes dolphins even resorted to plucking feathers from pelicans if none were available (Brown & Norris, 1956). While such catch and release behavior is common among wild delphinids

during prey handling and play (e.g., Mann & Smuts, 1999; Mann, Sargeant, & Minor, 2007; Whitehead & Mann, 2000), these captive individuals employed water jets and drains in a novel way. Unfortunately, nothing is known about the cognitive processes that lead in these behaviors so we cannot say for certain whether or not they are creative, but they do appear to be clever.

Some odontocetes also manipulate objects to create effects and/or create objects of their own to manipulate and play with. For example, Paulos et al. (2010) describe how some bottlenose dolphins tow inflatable pool toys around their tank, effectively creating a pressure wave which the dolphins can then surf. Probably the best captive example of creative and innovative object manipulation in play comes in the form of bubbles. Amazon River dolphins (*Inia geoffrensis*), belugas, and bottlenose dolphins have all been seen creating and playing with bubbles in captivity in diverse ways (Paulos et al., 2010). Amazon River dolphins use sticks and brushes to strike the water's surface to produce bubble curtains (possibly a modification of their wild behavior described later), which they then swim through or lie inside. They sometimes create curtains for each other and even rub one another with their bubble-creating brushes (Gewalt, 1989; Renjun, Gewalt, Neurohr, & Winkler, 1994). In the absence of brush or stick tools, they create bubble rings by releasing air from their blowhole (Gewalt, 1989). Belugas create bubble rings with their mouths (Delfour & Aulagnier, 1997), while bottlenose dolphins do so with both their blowholes and mouths, often in combination with other elaborations such as injecting air into vortices they created (Marten, Shariff, Psarakos, & White, 1996). Individuals also interact with bubbles in a diversity of ways from simple bubble biting and moving, to more complex bubble splitting and joining (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Marten et al., 1996; McCowan, Marino, Vance, Walke, & Reiss, 2000; Paulos et al., 2010). Much of this behavior appears to be planned as bottlenose dolphins monitor bubble quality and anticipate bubble movement (McCowan et al., 2000). Some authors have suggested that bubble techniques might be passed down through social learning and represent traditions or perhaps a "[bubble] ring culture" (Marten et al., 1996). While creating and playing with bubbles in and of itself may be common and not represent an innovation, the great diversity of ways in which odontocetes create, modify, and manipulate their bubbles suggests their behavior is the direct result of some underlying cognitive process and thus, in addition to representing their innovative abilities, speaks to their creativity.

As noted earlier, delphinids are well known for the imitative abilities, and they often employ these during play. Dolly's milk smoking (Tayler & Saayman, 1973) is particularly striking because Dolly was only around 6 months old at the time and inhibited her normal

swallowing behavior to instead release milk into the water. It seems plausible to infer that Dolly's behavior was the direct result of creative cognition, but Dolly was not the only imitator Taylor and Saayman observed in their study. Haig, one of Dolly's tank mates, regularly imitated the resident cape fur seal's (*Arctocephalus pusillus*) swimming, sleeping, and even grooming behavior, all of which were quite awkward and unnatural for Haig. She also appeared to imitate the behavior of skates, turtles, and penguins. Meanwhile, the male in the group, Daan, regularly imitated the behavior of human divers. On one occasion, after observing divers clean algae off of the underwater viewing port in his tank, Daan was seen using a seagull feather to scrape at the glass while mimicking the sounds and slow stream of bubbles produced by divers. Over the course of 54 days, Daan used food-fish, sea slugs, stones, and paper to keep the window clean and aggressively defended his new found territory. He even mimicked divers' hand positions by placing his pectoral fin on the window when cleaning. Later, Haig also attempted to clean the window and was actually given a brush to do the job but failed to hold the tool correctly. Bottlenose dolphins are not alone in their ability to imitate other species. [Kritzler \(1952\)](#) observed the same pilot whale that invented the flotsam-drain game attempt to mimic bottlenose dolphins who used their rostra to spear and throw inflatable inner tubes. Limited by his morphology (a short rostrum), after several failed attempts the whale began to use his pectoral fin to spear and play with the inner tube instead. It is true that intraspecific imitation may require very little, if any, innovation or creativity, but interspecies imitation is different. Such behavior requires individuals to not only first map their bodies onto the anatomy of a sometimes very different model, they must then create analogous behaviors within their own anatomical limits. Thus, these types of behaviors represent innovations and since many likely involve analogous cognitive mapping, also indicate some level of creativity.

Vocal Communication

Cetaceans have extraordinarily diverse communication systems ([Tyack, 2000](#)), aspects of which speak to their innovative and creative abilities. The strongest example is the signature whistle. During the 1960s, Melba and David Caldwell recorded the vocalizations of captive bottlenose and common dolphins (*Delphinus delphis*) and noticed that each individual appeared to have its own distinct whistle contour, which they appeared to develop within the first months of life ([Caldwell & Caldwell, 1965, 1968, 1979](#)). They called these vocalizations signature whistles and hypothesized that they might be used for

individual identification. Later, evidence of signature whistles was found in captive Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Caldwell & Caldwell, 1971), Atlantic spotted dolphins (*Stenella plagiodon*) (Caldwell, Caldwell, & Miller, 1973), and most recently, Pacific humpback dolphins (*Sousa chinensis*) (van Parijs & Corkeron, 2001). In these studies, signature whistles were recorded when individuals were isolated, usually for medical attention, a period in which an individual's signature whistle constitutes about 94% of its vocalizations. This led the Caldwells to further hypothesize that signature whistles might be used for maintaining group cohesion (Caldwell, Caldwell, & Tyack, 1990). In free swimming captive bottlenose dolphins, Janik and Slater (1998) found that individuals tended to produce signature whistles when one group member voluntarily isolated itself, lending further support to the group cohesion hypothesis. More recent evidence also supports the individual identification and vocal labeling hypothesis. For example, Bruck (2013) found that bottlenose dolphins in aquaria can remember each other's signature whistles even when separated for over 20 years. Some investigators have contested the presence of signature whistles (e.g., McCowan & Reiss, 2001), but more recent evidence from wild bottlenose dolphins provides fairly unequivocal support for both the presence of signature whistles and their importance in communication (reviewed in Janik & Sayigh, 2013). In fact, as we will discuss, field studies not only provide a wealth of information on signature whistles, they also indicate that every individual engages in true innovation during the first year of life, although the underlying cognitive processes are not known. What is somewhat unique here among animal innovations is that in order for a signature whistle to function as an individual identifier, it *cannot* spread through the population, although signature whistle copying occurs, possibly as a way to address conspecifics (Janik & Slater, 1998; Tyack, 1986). Thus, with every animal a signature whistle innovation is born and dies.

Foraging

While captive animals are usually well fed, some individuals seem to have invented novel ways in which to supplement their diet. For example, in addition to imitating other animals in her tank, Haig also imitated human divers in order to obtain food (Tyler & Saayman, 1973). After several days of closely observing divers scrape sea lettuce (*Ulva* sp.) off the tank floor, Haig scraped the tank floor with the divers' tool herself and ate the sea lettuce that came loose. After the scraper was taken away, she found a piece of broken tile to do the job. Later, her tank mate Lady Dimple learned the behavior and both dolphins

continued to forage in this way until all tiles were removed from the tank. A few decades earlier at Marineland of the Pacific, bottlenose dolphins Frankie and Floyd were observed attempting to capture a moray eel (*Gymnothorax mordax*), which they had trapped by positioning themselves on either side of a crevice the eel was hiding in (Brown & Norris, 1956). At some point, one of the dolphins left to capture a scorpion fish (*Scorpaena guttata*), and upon its return, poked the eel with the fish's sharp, venomous spines. The eel vacated the crevice and was quickly caught, although not consumed. Meanwhile, at Marineland of Florida, a young male bottlenose dolphin was observed attempting to coerce a large red grouper (*Epinephelus morio*) out of a rock crevice using dead squid and fish food as bait. Captive killer whales (*Orca orcinus*) have also been seen using their food to bait live prey especially gulls (Kuczaj, Lacinak, Garver, & Scarpuzzi, 1998; Noonan, 2005). While all these behaviors likely constitute innovations, Frankie and Floyd's eel poking is perhaps the most intriguing and seems likely to involve creative cognition.

Testing for Innovation

While these anecdotes provide some fairly convincing evidence that odontocetes are creative and capable innovators, most of the systematic research on cetacean creativity and innovation comes from Louis Herman's Kewalo Basin Marine Mammal Laboratory in Honolulu, Hawaii, which in its 30 plus years, provided the most comprehensive view of dolphin cognition to date (Herman, 2012a). By training their dolphins to respond to auditory and gestural cues, Herman and colleagues tested dolphins on a variety of tasks carefully constructed to probe their cognitive abilities. Animals were trained to perform various actions such as *fetch*, *leap over*, *swim under*, etc. often in conjunction with various items such as *ball*, *hoop*, and *frisbee* (Herman, 2010). In most of Herman's studies, objects were positioned appropriately to allow the dolphins to perform the requested action. However, on at least one occasion, a female dolphin named Akeakamai (Ake) was asked to perform behaviors that were impossible given the current orientation of the objects in her tank. She spontaneously solved this problem by rearranging the items in a way that would allow her to complete the requested action (Herman, 2006). For example, if asked to swim through a hoop lying flat on the bottom of the tank, Ake would lift the hoop into an upright position and swim through it. She also spontaneously rearranged objects in her tank to help in cleaning up after an experimental session. At the end of a session, trainers gave Ake the *fetch* gesture, which asks her to retrieve all the objects in her tank. Rather

than fetching the objects one by one as she was trained, Ake “round up” several objects at once, effectively inventing a novel strategy for efficiently cleaning up her tank (Herman, 2006).

Ake again showed her innovative and creative skills when she was asked to perform a behavior with an object that was absent from her tank. Ake was taught to press one of two paddles corresponding to either yes or no depending on whether or not an object was present in her tank (Herman, 2006). During one experiment, she was asked to bring one object over to another that was missing, and she responded by retrieving the first object and bringing it to the no paddle (Herman, 2006), essentially coming up with a way to communicate to the experimenter that the task could not be completed. This was not the only time she came up with a novel way to communicate with trainers. Occasionally wind blew debris into Ake’s tank, after which she would produce a distinct, loud whistle. Eventually staff learned that Ake seemed to be calling to them to come remove the debris, which she had brought to the side of the tank (Herman, 2006). Importantly, all of Ake’s responses above were spontaneous, untrained, unexpected, and novel, and it seems likely that at least some involved creativity.

We have already noted that delphinids are impressive imitators, and Herman’s dolphins are no exception. In trying to teach two young dolphins Hiapo and Elele to associate specific behaviors with gestures, trainers gave a gesture and then immediately modeled the behavior for the dolphins. While neither dolphin learned the gestural cues, both imitated their human trainers’ actions, sometimes with remarkable accuracy on the first try (Herman, 2002). This somewhat accidental result was examined in more detail later by teaching Ake and Phoenix a gesture for *mimic* and testing their ability to imitate human models. Like Haig and Daan’s behavior, these cross-species imitations require abnormal body mapping meaning they are both creative and innovative. From these studies and others, we know that bottlenose dolphins are exceptional imitators and even appear to have a conceptual level understanding of imitation (Herman, 2002).

While the above studies corroborate some of the anecdotes presented earlier, no study does so better than the famous “Creative Porpoise” experiment conducted at Sea Life Park at the Makapuu Oceanic Center in Hawaii in the 1960s.¹ In their study, Karen Pryor (also see Chapter 17) and colleagues used a paradigm in which “only those actions will be reinforced, which have not been reinforced previously” (Pryor, Haag, & O’Reilly, 1969). The technique was initially trialed on

¹See video clip at http://reachingtheanimalmind.com/chapter_05.html.

Malia, a female rough-toothed dolphin (*Steno bredanensis*), during regular dolphin shows. After several days of reinforcing one unique behavior each show, Malia exhausted her normal repertoire and began showing signs of frustration. However, on the morning of day four, Malia seemed to spontaneously “get it” and upon entering the main tank, quickly circled around to build up speed, rolled onto her back and stuck her tail fluke in the air and coasted as if she were sailing. She had created a new behavior, one she could not have practiced in her small holding tank, and one Pryor and colleagues had never seen before (Pryor, 2009). After this breakthrough, Malia continued to come up with novel behaviors. Perhaps one of the more interesting examples is what Pryor calls Malia’s “art project” (Pryor, 2009). Showing off her sketching abilities, Malia once used her dorsal fin to draw “beautiful looping lines” in the silt on the bottom of her tank (Pryor, 2009). Pryor et al. (1969) followed up on their initial trials with a more detailed study using a new female rough-toothed dolphin, Hou. The same general procedure was used in that only one novel behavior was reinforced per training session, and after 16 sessions Hou too seem to grasp the concept. In fact, by session 33 Hou’s behaviors became so complex and novel that the experimenters had trouble discriminating and describing them, so the study had to be stopped. To examine just how unique some of these behaviors were, Pryor et al. (1969) asked facility staff to rank Hou’s behaviors according to how often they spontaneously occurred in other captive cetaceans. While some of Hou’s behaviors had been commonly observed in a variety of species, 11 of Hou’s 16 behaviors had either rarely been observed in any species, only observed in *Stenella* spp., or had never been observed by staff before in any cetacean. After the experiment was over, Hou was introduced into the dolphin show and trained, like Malia, to perform certain behaviors in response to specific cues. However, if trainers took up the position used during the creative experiments, both Malia and Hou would readily produce novel behavior, demonstrating their remarkable flexibility in being able to switch from producing behavior under specific stimulus control, to that which requires their own creative input.

While some have questioned the validity of Pryor’s et al. (1969) original findings (e.g., Holth, 2012), similar methods have since been used to elicit novel behavior in a variety of other species (dogs, *Canis lupus familiaris*; cats, *Felis catus*; horses, *Equus ferus caballus*; parrots, Psittaciformes; gorillas, *Gorilla gorilla gorilla*; budgerigars, *Melopsittacus undulates*; and walruses, *Odobenus rosmarus*) (Manabe, 1997; Manabe & Dooling, 1997; Pryor, 2004a, 2004b, 2006, 2009; Schusterman & Reichmuth, 2007), including bottlenose dolphins (Herman, 1991; Kuczaj & Eskelinen, 2014). Herman and colleagues taught bottlenose dolphins a *create* gesture, which asked for a behavior different from the

preceding behavior (Braslau-Schneck, 1994; Herman, 1991, 2002, 2006, 2010; Mercado, Murray, Uyeyama, Pack, & Herman, 1998; Mercado, Uyeyama, Pack, & Herman, 1999). This is slightly different than Pryor's et al. (1969) study in that creative behavior is now under control of a gesture, allowing trainers to repeatedly ask for new behaviors within a single trial. Herman's dolphins were also taught a *repeat* gesture, which asked them to repeat the behavior they had just performed. Elele and Hiapo successfully learned both the *repeat* and *create* commands, and could even repeat previously self-selected behavior (Herman, 2002; Mercado et al., 1998, 1999). Furthermore, the two were able to create new behaviors together. After individually mastering the *create* sign, the dolphins were given the *tandem* sign (previously used to elicit synchronous trainer selected behavior) and *create* sign in conjunction (*tandem + create*) to see how they would respond. After a brief period of side-by-side swimming, the dolphins executed a new behavior in almost perfect synchrony (Braslau-Schneck, 1994; Herman, 2002, 2006). Later, Ake and Phoenix also successfully learned the *tandem*, *repeat*, and *create* signs and could use them in combination (Braslau-Schneck, 1994). While, the *create* command does not actually require completely novel behavior, the only restriction being that the behavior not be identical to the one immediately preceding it, all dolphins in Herman's studies regularly came up with never before seen behaviors, both individually and in tandem (Braslau-Schneck, 1994; Herman, 2002, 2006). More recently, Kuczaj and Eskelinen (2014) examined individual variation in response to a *create* cue, which they prefer to call *vary*, using bottlenose dolphins at Dolphin Cove in Key Largo, Florida. Leo, the youngest of the three males in their study, exhibited more novel, more complex, and higher energy behaviors than the older adults Alfonz and Kimbit. Kuczaj and Eskelinen (2014) suggest this could be due to differences in cognitive style and strategy, but at around 10 years old, Leo was much younger than the two 20-year-old adults so his higher performance could also be the result of differences in motivation, trainability, and fatigue that may come with age. Regardless, these *create/vary* studies not only demonstrate that dolphins are remarkably innovative and creative and can be so on command, they seem to grasp the concept of novelty itself (Herman, 2006).

Given this brief review in captivity, what can we conclude about cetacean innovation and creativity? Since so few have been kept in captivity, nothing about mysticetes, but odontocete appear to innovate in a variety of contexts. Most often these skills are used in play, rather than in foraging or communication. This is not surprising since captive animals are encouraged to play, but have little forage demands and experience an unnatural social environment with few incentives for interspecific communication. While this situation poorly represents the

conditions faced by wild odontocetes, the anecdotes and experiments discussed *do* suggest that many odontocetes are highly innovative and sometimes creative, skills that prove useful in the wild as discussed next.

INNOVATIONS AT SEA

The study of marine organisms, even at the most basic level, lags behind that of terrestrial species for obvious logistical reasons. Cetologists at least have the advantage that their study subjects are large and breathe air, but this provides quite literally only a surface level understanding of cetacean behavior. The end result is that compared to those on terrestrial fauna, field studies on marine fauna are fewer, suffer greater observational biases, and tend to be more descriptive in nature. Recognizing these limitations is critical when examining innovative and creative behavior. For example, we know very little about deep, underwater behavior, particularly that which occurs far offshore, in the oceanic zone, and even near shore, at the surface we usually can only observe behavior at a coarse grain (Russon, 2003). In all, these limitations almost certainly lead us to underestimate the prevalence of innovative and creative behaviors in wild cetaceans. Nevertheless, there are many examples of rare, unusual, novel, and/or atypical species behavior scattered throughout the literature that provide insight into how cetacean innovative and creative abilities might have evolved and are used in the wild. As before, we describe these within their greater functional contexts.

Play

Like those in captivity, free ranging cetaceans demonstrate a great diversity of play behaviors, many of which can be considered innovative and some, creative. As before, some include intraspecific imitation, and thus likely involve creativity. For example, Würsig (2008) witnessed a bottlenose dolphin off the coast of the Bahamas mimic the awkward swimming of a snorkeling tourist. However, most examples of innovative play behavior in the wild involve cetaceans interacting and playing with novel objects (Paulos et al., 2010). As before, simply manipulating and playing with such objects may not be all that innovative, but the details concerning a few of these behaviors inform us on innovation and creativity. Examples exist for both odontocetes and mysticetes, and include some mysticete—odontocete interactions.

Many wild delphinids regularly interact with birds in a playful manner (Heubeck, 2001; Hewitt, 1986; Mann & Smuts, 1999; Würsig, 2008). For example, after foraging on anchovy schools off the coast of Argentina, some dusky dolphins (*Lagenorhynchus obscurus*) have been seen carefully grabbing the dangling legs of unsuspecting gulls, quickly surging underwater, and then releasing the gulls', effectively dunking the birds. The dolphins are very gentle in their grasp, never causing any harm, and simply appear to be having a little fun with their feathered counterparts (Würsig, 2008). As yet unreported elsewhere, this gull-dunking game resembles some of the innovative play behavior of captive delphinids described earlier.

Another possible example of play innovation among wild odontocetes comes from the "southern resident," fish-eating community of killer whales in Puget Sound, Washington. In 1987, a female from a pod known as K-pod was observed carrying a dead salmon around on top of her head (Baird, 2002; Whitehead, Rendell, Osborne, & Würsig, 2004). Within that same year, the behavior quickly spread to two additional pods in the southern resident community, but disappeared from the community shortly after. While the function of dead salmon carrying is unknown, some suggest it may have been a cultural fad (Baird, 2002; Whitehead et al., 2004), although here we consider it in the context of play since it appears to have no immediate purpose. This example not only demonstrates potential innovative play behavior, but also its horizontal transmission and eventual disappearance.

Free ranging mysticetes also play with objects in ways that suggest innovative behavior, with bowhead whales (*Balaena mysticetus*) providing probably the strongest example. During the boreal summer and fall, bowhead whales in the Beaufort Sea can be seen interacting with floating logs in rather "artistic" ways (Würsig, 2008, p. 887). This includes nudging, propelling, and dunking logs using their flippers and tails, but more impressively, balancing logs on their backs or bellies and even adjusting their body position to account for ocean swell (Würsig & Dorsey, 1989; Würsig, 2008). Similar log play might also occur in sperm (*Physeter macrocephalus*) (Nishiwaki, 1962) and perhaps humpbacks whales (*Megaptera novaeangliae*) (Couch, 1930). Playing with logs itself is likely not all that innovative, but the diversity of ways in which whales manipulate their log toys may indicate some creative processes is at work.

Occasionally odontocetes and mysticetes interact with each other in ways that demonstrate their innovative abilities. For example, recently off the coast of Hawaii Deakos, Branstetter, Mazzuca, Fertl, and Mobley (2010) observed humpback whales using their rostra to lift bottlenose dolphins entirely out of the water, after which the dolphins slid down the whales' backs and entered the water. This behavior was observed on two occasions and in both instances neither the dolphin nor the humpback

behaved aggressively. Given this, and that the behavior has no obvious function, it is presumed to be a form of interspecific play and may constitute a cross-species innovation. Other odontocete-mysticete interactions seem to be more one sided. Bottlenose and dusky dolphins have been known to “coerce” large whales (balaenids and sperm whales) into helping them surf by swimming on either side of the whales’ eyes perhaps to agitate them (Würsig, 2008). After a while, the whales appear to become irritated and surge forward, creating large waves that the dolphins eagerly surf. Perhaps dolphins’ use of pool toys to create waves as noted earlier is a modification of this behavior adapted to a captive lifestyle. While intent is not known, the dolphins are probably the innovators, and the whales, just the object of their harassment.

Cetaceans also interact with humans in playful ways that suggest innovation and creativity. Many cetologists have firsthand experience with this, as wild delphinids often invent and play games with their scientific audience (e.g., passing seagrass or leaves back and forth) (Johnson & Norris, 1994; Mann & Smuts, 1999). However, one of the most well-known human–cetacean interactions involves gray whales. In 1975, off the coast of Baja California, Mexico in Laguna San Ignacio, Gilmore (1976) observed several gray whales that behaved unusually curious and “friendly” toward boats. Several whales deliberately approached whale-watching vessels and allowed tourists to stroke them. At the time, such behavior was quite surprising since less than a century ago these long-lived mammals were referred to as “devil fish,” a name attesting to their violent interactions with whalers. A later study confirmed that while the so called “friendly” phenomena may have been around slightly earlier (1960s), the behavior seemed to be relatively new (Jones & Swartz, 1984). This study also found that by 1982, the friendly behavior had rapidly spread throughout the Baja California region, and even to the northern end of the whales’ migration route, off Vancouver Island and in the Bering Sea (Jones & Swartz, 1984). Friendly whales of both sexes and all ages, individually and in groups, approach tour vessels, usually from the stern and mainly when the engine is in neutral perhaps to investigate the source of the engine noise (Jones & Swartz, 1984). In addition to allowing tourist to pet them, the whales often blow bubbles under the boats, produce a variety of vocalizations, and probe and lift the boats, occasionally even knocking passengers overboard (Jones & Swartz, 1984). Some whales seem particularly attached to boats and will follow them for an entire day, even at speed, and repeatedly do so year after year (Jones & Swartz, 1984). Although this behavior does not appear all that creative, like dead salmon carrying in killer whales, it illustrates how innovations that likely have little impact on fitness can rapidly spread throughout a population, even across some 5,000 km or more of ocean.

Vocal Communication

Research on wild cetacean vocal communication may suffer the greatest from the logistical difficulties of studying at sea, with the most notable obstacle being one of the first steps in studying vocal communication: identifying the vocalizer. Most terrestrial species produce visual cues that indicate they are vocalizing and, even in the absence of such cues, researchers can often localize the sound with their own ears. However, cetaceans produce very few, if any, visual cues and it is impossible to localize sound underwater without sophisticated hydrophone arrays. That said, in the last 25 years or so great advances in acoustic technologies have provided a wealth of information on cetacean vocal communication, and much of this work points to communication as a fruitful domain in which to examine cetacean innovation and creativity.

In the two largest odontocetes, killer and sperm whales, neighboring groups of individuals exhibit distinct vocal repertoires called dialects (Ford, 2008). Among killer whales, dialects seem to be present at two hierarchical social levels, both based on matrilineal relatedness. Smaller stable groups known as pods have distinct acoustic repertoires but share a portion of this repertoire with several other related pods to form what is known as an acoustic clan (Ford, 1991; Nousek, Slater, Wang, & Miller, 2006). In contrast, sperm whale dialects (termed coda dialects) also differ among matrilines, but are only distinct at a higher clan level (Whitehead, 2003). In both taxa, dialects are thought to be socially learned within matrilines and function in communication and maintaining group cohesion (Ford, 1991; Miller, 2002; Weilgart & Whitehead, 1993). In killer whales, changes in dialects have been documented and appear to mostly be the result of cultural drift (Deecke, Ford, & Spong, 2000). However, some evidence suggests that cultural selection, possibly through inbreeding avoidance, plays a role in the evolution of more complex vocal calls (Barrett-Lennard, 2000; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Although no long-term changes in sperm whale coda dialects have been recorded (Rendell & Whitehead, 2005), high dialect differentiation and low genetic differentiation across ocean basins suggests coda dialects have changed through time and are subject to cultural evolution (Lyrholm, Leimar, Johannesson, & Gyllenstein, 1999; Rendell & Whitehead, 2003). In both sperm and killer whales, a single change in a group's dialect, if functional, could constitute an innovation, but whether or not this is the case is unclear. Regardless, most evidence indicates that these vocal changes are not the result of some creative process, but rather errors in vocal copying (Deecke et al., 2000; Yurk et al., 2002).

While sperm and killer whale dialects may hint at vocal innovation, signature whistles provide direct evidence of innovative behavior in

wild cetaceans. Since the time of the Caldwells' initial work in captivity, evidence of signature whistles has been documented in wild bottlenose dolphins (Gridley et al., 2013; Smolker, Mann, & Smuts, 1993), Guiana dolphins (*Sotalia guianensis*) (Duarte de Figueiredo & Simão, 2009), narwhals (*Monodon monoceros*) (Shapiro, 2006) and possibly pilot whales (Sayigh, Quick, Hastie, & Tyack, 2013). In bottlenose dolphins, field data continue to support the hypothesis that signature whistles aid in group cohesion and communicate individual identification. For example, in Sarasota Bay, Florida bottlenose dolphins increased signature whistle production in larger groups and during social behavior (Cook, Sayigh, Blum, & Wells, 2004), and in Shark Bay, Australia bottlenose dolphin calves produced signature whistles primarily when separated from their mother, particularly at far distances and near the end of separations (Smolker et al., 1993). In addition, wild bottlenose dolphins seem to recognize their own signature whistles (King & Janik, 2013), and copy the whistles of close associates (mothers and calves, alliance partners) possibly as a way to label and address conspecifics (King, Sayigh, Wells, Fellner, & Janik, 2013). Vocal copying also seems to be important in the development of signature whistles. In Sarasota Bay, Florida calves appear to model their signature whistles from those of their conspecifics, but modify these to invent their own distinct, new whistles (Fripp et al., 2005). However, males and females seem to differ in terms which model they use. Male calves' signature whistles more closely resemble those of their mothers' compared to females', possibly to help avoid inbreeding (Sayigh, Tyack, & Wells, 1995; Sayigh, Tyack, Wells, & Scott, 1990). Male signature whistles are also less stable than females, often converging with those of their male alliance partners in adulthood (Smolker & Pepper, 1999; Watwood, Tyack, & Wells, 2004). However, for both male and female calves there is low similarity between mother and offspring signature whistles, further suggesting that signature whistles are not genetically determined, but rather individually and socially learned (Janik & Sayigh, 2013). In all, signature whistles clearly serve an important social function, and are somewhat unique among animal communication signals in just how individually distinct they are.

Foraging

Cetaceans exhibit a great diversity of foraging behaviors in the wild, many of which speak to their innovative and creative skills. There are many examples of cetaceans interacting with fishers or tourists in novel ways to obtain food. For example, dolphins and whales in numerous locations depredate long-lines (Ashford, Rubilar, & Martin, 1996;

Hamer, Childerhouse, & Gales, 2012; Nolan, Liddle, & Elliot, 2000; Purves, Agnew, & Balguerias, 2004; Visser, 2000; Yano & Dahlheim, 1995), steal prey from traps or fish farms (Kemper et al., 2003; Noke & Odell, 2002), and follow trawlers or trammel nets in hopes of consuming stray prey or discards (Chilvers & Corkeron, 2001; Gonzalvo, Valls, Cardona, & Aguilar, 2008; Jefferson, 2000; Leatherwood, 1975; Pennino, Mendoza, Pira, Floris, & Rotta, 2013). In many cases these behaviors start out at low frequency, but rapidly spread to the rest of the population, possibly indicating an initial innovation event and its subsequent social transmission among sympatric cultural units or clusters (e.g., Chilvers & Corkeron 2001; Donaldson, Finn, Bejder, Lusseau, & Calver, 2012; Fearnbach et al., 2013; Whitehead et al., 2004). Despite the risks of becoming bycatch themselves, these cetaceans benefit by avoiding the energetic costs of long prey chases and deep dives.

Some cetacean–fisher interactions have become elaborated into what can be called cooperative foraging. Famously, for 80 years the “killer whales of Eden” assisted whalers during hunts of humpback and southern right whales (*Eubalaena australis*) in Twofold bay, Australia (Dakin, 1934; Jefferson, Stacey, & Baird, 1991). In exchange for the help, whalers allowed the killer whales to feed on the favored tongues and “lips” in an agreement known as “the law of the tongue” (Brady, 1909). In coastal fisheries off Laguna, Brazil, bottlenose dolphins and fishers regularly cooperate to catch schools of mullet (*Mugil* spp.) (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Pryor, Lindbergh, Lindbergh, & Milano, 1990; Simões-Lopes, Fabián, & Menegheti, 1998). Here, dolphins drive mullet toward shore and after a series of more subtle movements, “signal” with tail and head slaps where the fishers should throw their nets (Simões-Lopes et al., 1998). This foraging tactic appears to be socially facilitated as dolphins who perform the behavior associate more than those who do not, leading some to suggest that the behavior has been passed down for over 160 years (Daura-Jorge et al., 2012; Pryor et al., 1990). In Myanmar, a similar cooperation between dolphins and fishers exist. For over 130 years fishers have used a variety of signals to advertise their interest in cooperating with Irrawaddy dolphins (*Orcaella brevirostris*), who then herd fishes into tight schools for easy netting (Smith, Tun, Chit, Win, & Moe, 2009). In all well-documented cases, both fishers and dolphin appear to benefit with higher catch rates and/or volumes of fishes (Simões-Lopes et al., 1998; Smith et al., 2009). Although the underlying cognition and transmission of these behaviors is not known, they illustrate how innovations between humans and wild animals can develop and persist for over a century.

Probably the most common form of human–cetacean interaction involves recreational fishers directly feeding dolphins, which has

resulted in extensive begging behaviors and harm to wildlife in southeastern United States (e.g., [Samuels & Bejder, 2004](#)) and several parts of Australia ([Donaldson et al., 2012](#); [Foroughirad & Mann, 2013](#)). Although these animals are making use of a novel food resource, such feeding is not particularly unusual ([Orams, 2002](#)). However, in some locations dolphin provisioning has taken other forms and involves more elaborated behaviors that are not typical. In Monkey Mia, Shark Bay, Australia, a small number of bottlenose dolphins (mostly female and from 3 matriline) have been provisioned by tourists since the 1960s ([Foroughirad & Mann, 2013](#)), a program that is now supervised and strictly regulated by Western Australia's Department of Parks and Wildlife. In the 1980s, several unusual behaviors emerged among the provisioned dolphins ([Smolker, 2001](#)); one, started by a young male named Snubnose, involved a posture in which a dolphin arches its back, holds its tail and head out of the water, and plants its pectoral fins and belly on the seafloor ([Figure 4.1](#)). This gesture soon spread to other provisioned dolphins and is still seen today, even by young calves that are not fed (JM, personal observation). Another unusual behavior involves "gift-giving." Even though dolphins do not share prey with each other ([Mann et al., 2007](#)), in Monkey Mia they occasionally attempt to give fishes to humans, a behavior that has been seen ~30 times over the course of 27 years. In each case, a dolphin brings a large fish to the beach and drops or holds it gently next to a person, sometimes nudging him or her repeatedly with the fish. In the most striking example, after



FIGURE 4.1 A male dolphin named Snubnose performing a begging gesture near Monkey Mia, Australia in the 1980s, a behavior that spreads and persists to this day among other provisioned dolphins. *Photo taken by Janet Mann.*

months of a ranger trying to initiate a 6-year-old female named Piccolo into the provisioning program, she finally accepted a fish and swam off. The next day, she caught a large whiting (*Sillago* sp.), brought it into the beach, and spent 20 min trying to get that same ranger to take it, even rising up on the ranger's chest with the fish in her mouth (JM, personal observation). It is tempting to speculate that because humans were sharing fishes with her, Piccolo was trying to reciprocate, a behavior that could be considered creative. In the end, the ranger did not take the fish and Piccolo swam off. After that, she refused fish offers for the next 5 years until she had her own offspring and was perhaps hungry enough to give it a try. Food gift-giving has occurred at human dolphin provisioning sites elsewhere (Holmes & Neil, 2012), but to our knowledge, has otherwise not been reported between nondomesticated species and humans.

Some human–cetacean interactions may indirectly result in innovative foraging behavior. For example, whaling practices (Williams, Estes, Doak, & Springer, 2004), oil spills (Loughlin, 1994), and other human activities have depleted preferred prey of killer whales. From large whales to Steller sea lions (*Eumetopias jabatus*), harbor seals (*Phoca vitulina*) (Loughlin, 1994), and eventually sea otters (*Enhydra lutris*) (Estes, Tinker, Williams, & Doak, 1998; Williams et al., 2004), killer whales turned to smaller and smaller prey to meet their energetic demands (but see DeMaster et al., 2006). Although the causes have been debated, these killer whales are utilizing both new resources and new foraging tactics to obtain them. Such behavior however, is not surprising since killer whales are known to consume a great diversity of prey (Jefferson et al., 1991) (although see later for discussion of foraging tactics). Here, prey switching may simply constitute a change in expression of an existing behavior and involve little creativity or innovation *per se*. Humpback whales have also responded to prey collapses over the decades by switching diets from herring (*Clupea harengus*) to sand lance (*Ammodytes americanus*), and in the process, foraging tactics from lunge feeding to lobtail feeding and bottom-side rolling (Allen, Weinrich, Hoppitt, & Rendell, 2013; Read, 2001; Ware et al., 2014; Weinrich, Schilling, & Belt, 1992). Lobtail feeding is characterized by whales striking their tail on the water surface several times, followed by creating bubble-streams, but the whales also scrape along the bottom where sand lance congregate (Ware et al., 2014). This behavior contrasts with the more typical lunge-feeding pattern, and is argued to have been culturally transmitted given the pattern of diffusion (Allen et al., 2013). Although this striking shift in foraging tactics suggests flexibility and social transmission among whales, sand lance feeding clearly occurred at least at low frequencies well before spreading (Hain, Carter, Kraus, Mayo, & Winn, 1982; Weinrich et al., 1992).

Clearly direct (e.g., tourism, fishing, feeding) and indirect (e.g., prey collapse) human impacts create new challenges for which cetaceans have innovative responses, but cetaceans also naturally exhibit diverse and innovative foraging tactics. Both humpback and minke whales have been intensively observed at some locations so their foraging tactics are relatively well known. Humpback whales engage in bubblenet and bubblecloud feeding (Hain et al., 1982; Ingebrigtsen, 1929; Jurasz & Jurasz, 1979; Wiley, Ware, & Bocconcelli, 2011) where they cooperatively or singly create circular walls of bubbles or bursts of bubbles that form a cloud to aid in prey capture (Hain et al., 1982; Wiley et al., 2011). Given the apparent cooperation between individuals that engage in bubblenet feeding, some have suggested that the behavior is socially learned (Clapham, 2000; Weinrich, 1991; Weinrich, Rosenbaum, Scott Baker, Blackmer, & Whitehead, 2006) and possibly a case of tool use depending on one's definition (Mann & Patterson, 2013). Similar to the creative use of bubbles described earlier, the cooperation and planning that appears to be involved indicates that bubblenet feeding may involve some creative cognition and qualify as an innovation.

Humpback whales are not alone in their use of bubbles during foraging as such behavior has been previously reported in killer whales (Sigurjónsson, 1988; Similä & Ugarte, 1993) and Atlantic spotted dolphins (*Stenella attenuate*) (Fertl & Würsig, 1995). For example, in a behavior that may also involve creative cognition and constitute innovative tool use, killer whales have been observed releasing bubbles "downward" toward stingray prey possibly to startle them from their burrowed location (Visser, 1999). In fact, killer whales exhibit a great diversity of feeding tactics within and across sites (Baird, 2000; Jefferson et al., 1991). Many of these tactics are thought to be socially learned traditions passed on primarily through matrilineal lines (Riesch, Barrett-Lennard, Ellis, Ford, & Deecke, 2012). Most famous of these occur with the two ecotypes of killer whales in the Pacific Northwest: the "resident" or fish-eating killers whales (which eat predominantly salmon, *Oncorhynchus* spp.) and the "transient" or mammal-eating killer whales (which eat predominantly harbor seals) (Baird, 2000). Over 40 years of study has revealed that these ecotypes differ genetically and in diet, ranging patterns, vocal and social behavior, and pod structure (Baird, 2000; Dahlheim & White, 2010; Deecke, Nykänen, Foote, & Janik, 2011; Ford, Ellis, Barrett-Lennard, Morton, & Balcomb, 1998; Herman et al., 2005; Saulitis, Matkin, Barrett-Lennard, Heise, & Ellis, 2000). Although occasionally near each other, they do not interact or breed, and it has been suggested that they are currently undergoing speciation (Riesch et al., 2012). More recently, studies have revealed what is thought to be yet another Pacific Northwest ecotype, called the "offshores," that specialize in other fishes such as Pacific halibut (*Hippoglossus stenolepis*) and Pacific sleeper sharks (*Somniosus pacificus*),

but currently little is known about their social structure and behavior (Dahlheim et al., 2008; Ford & Ellis, 2014; Ford et al., 2011; Jones, 2006; Krahn et al., 2007).

The killer whales of the Pacific Northwest are not unique among killer whales in terms of their innovative and creative foraging behavior. At several disparate sites from Patagonia, the Faroes, to the Crozet Islands, killer whales beach or temporarily strand themselves to catch pinnipeds and occasionally seabirds (Bloch & Lockyer, 1988; Guinet, 1991; Guinet & Bouvier, 1995; Hoelzel, 1991; Lopez & Lopez, 1985). Within a population, members of some pods engage in the behavior while others do not. Sometimes the killer whales create pressure waves to help wash unsuspecting seals off the beach, or lunge suddenly out of the water and even synchronize their beaching to reduce the chances of prey escaping (Bloch & Lockyer, 1988; Guinet, 1991; Guinet & Bouvier, 1995; Hoelzel, 1991; Lopez & Lopez, 1985). Wave washing, singly and in coordinated groups, also occurs on ice floes in the Southern Ocean off Antarctica (Pitman & Durban, 2012; Smith & Siniff, 1981; Visser et al., 2008). These dramatic and planned attacks involve inspecting ice floes for preferred prey, Weddell seals (*Leptonychotes weddellii*), and recruiting fellow pod-members to aid in washing seals off the ice and into the water where they can be pursued. For larger floes, whales sometimes first use a wave to break the floes up and have even been observed lifting ice with their heads (Pitman & Durban, 2012). The variation in these attacks suggests that the killer whales' behavior is planned and adaptable to their changing circumstances. Like in the Pacific Northwest, killer whales in the Southern Ocean appear to represent several different ecotypes, one that specializes on seals, a second on penguins (Pitman & Durban, 2010), a third on minke whales, and a fourth on fishes (Pitman & Ensor, 2003). In the North Atlantic, this pattern again repeats itself with some pods specializing on marine mammals (Deecke et al., 2011; Foote, Newton, Piertney, Willerslev, & Gilbert, 2009), and others on fishes (predominantly Atlantic herring, *Clupea harengus*) (Similä & Ugarte, 1993; Similä, Holst, & Christensen, 1996). The striking feature within and across killer whale populations is that genetic and behavioral data suggest that many of these foraging innovations have become specializations, which are then matrilineally transmitted and can result in reproductive isolation and eventually speciation (Riesch et al., 2012).

Like killer whales, bottlenose dolphins also exhibit great diversity in their natural foraging behaviors, many of which can be considered innovative. Strand-feeding, similar to that described for killer whales above, occurs at several sites including South Carolina and Georgia (Duffy-Echevarria, Connor, & St. Aubin, 2008; Hoese, 1971; Rigley, VanDyke, Cram, & Rigley, 1981), Mexico (Silber & Fertl, 1995), Portugal

(dos Santos & Lacerda, 1987), Mozambique (for *Sousa plumbea*, Peddemors & Thompson, 1994) and Australia (Sargeant, Mann, Berggren, & Krützen, 2005). In all of these cases, dolphins either individually or collectively trap fishes (almost always mullet) by chasing them onto the shoreline, and then fully or partially lunge out of the water and onto the shore to catch their prey. Only certain individuals engage in this risky behavior, even though in some cases (e.g., Sargeant et al., 2005) other dolphins repeatedly witness these beaching dolphins successful catch prey. At each location, distinct variations of strand-feeding are evident. In Bull Creek, South Carolina, typically 3–4 dolphins cooperatively surge onto mudbanks to catch fishes (Duffy-Echevarria et al., 2008). In Shark Bay, only 6 dolphins currently engage in the behavior out of hundreds near shore (Sargeant et al., 2005; JM & EMP, personal observation), and usually do so individually even when they use the same beach simultaneously.

Other unusual foraging behaviors have been reported from most sites where bottlenose dolphins have been studied. For example, off the coast of Florida several forms of mud plume feeding have been seen, where dolphins either cooperatively (Torres & Read, 2009) or singly (Lewis & Schroeder, 2003) use their tails to create mud like “nets” around schools of mullet, which attempt to escape by leaping over the mud-ring, but end up in the dolphins’ waiting jaws. However, most of what we know about foraging innovations among wild bottlenose dolphins comes from one population, the Shark Bay Indian Ocean bottlenose dolphins, where we have documented over 20 distinct foraging tactics. In what is perhaps one of the most striking innovations among cetaceans, a subset of the Shark Bay bottlenose dolphin population perform a tool-use behavior known as sponging. This behavior was first discovered in 1984, when Rachel Smolker observed a dolphin named “Halfluke” with a marine sponge on her rostrum (Smolker, Richards, Connor, Mann, & Berggren, 1997). The cone-shaped sponge (*Echinodictyum mesenterinum*) was seen to fit over the dolphin’s beak (Figure 4.2) (Smolker et al., 1997) and hypothesized to act as protection when foraging. Since the 1980s, we have now identified dolphins using several other species of conical sponges (Mann & Patterson, 2013) and have further confirmed that sponges are used as tools during foraging to allow dolphins to exploit a unique niche (Krützen et al., 2014; Patterson & Mann, 2011). Sponging dolphins appear to detach basket sponges from the seafloor of deep (8–14 m) channels, and then wear these over their rostra for protection while probing rock, shell and other debris in search of prey, primarily barred sandperch (*Parapercis nebulosa*) (Patterson, 2012; Patterson & Mann, 2011). Five female spongers were recognized in the 1980s, but today over 100 have been documented (Mann & Patterson, 2013). While this increase is not due to the



FIGURE 4.2 A male dolphin named Dali foraging with a marine basket sponge (*Ircinia* sp.) in Shark Bay, Australia. Photo taken by Eric M. Patterson.

behavior's spread, just an expansion in research effort, we have documented the spread of sponging vertically, within matriline. Whereas daughters of spongers have over a 95% chance of becoming spongers, sons have only a 50% chance of doing so (Mann et al., 2008). Although spongers preferentially associate, the majority of their associates are nonspongers, but the behavior does not seem to spread horizontally (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012). In fact, only about 4% of the dolphin population uses this foraging method, which is restricted almost entirely to deep-water channels. Data indicate that sponging occurs in at least three sites in Shark Bay, the eastern gulf (Mann et al., 2008; Smolker et al., 1997), the western gulf (Kopps, Krützen, Allen, Bacher, & Sherwin, 2013), and a point 50 km north of both sites, near the point of the Peron Peninsula (Mann & Patterson, 2013). This could indicate three independent innovation events, given the strict matrilineal transmission and genetic haplotypes observed at the sites (Kopps et al., 2014; Krützen et al., 2005; Patterson et al., in preparation), or historical horizontal transmission of an initial sponging innovation. That said, spongers have only been sighted a maximum of 6 km from the channels where they "sponge," and since the three sponging locations are separated by more than this length of nonchannel habitat, mixing between the subpopulations would be rare (Mann & Patterson, 2013).

For the last 20 years, we have also periodically observed another potential foraging innovation called "shelling." In this behavior, dolphins retrieve the shells of large dead molluscs (*Syrinx aruanus* and *Melo amphora*) from the seafloor and then, at the water's surface, balance

and wave them around in what appears to be an effort to drain the shells and extract the prey hiding inside (Allen, Bejder, & Krützen, 2011; Mann & Patterson, 2013). In the eastern gulf, the same individuals, from only a few families, have been seen engaging in the behavior on more than one occasion. Currently, the nature of this innovation is not completely understood. We do not know whether dolphins chase fishes into the shells, happen upon shells with fishes inside them, and/or revisit or reuse the same “fish traps” repeatedly. Nevertheless, the fact that we have observed a few matriline repeatedly “shell” may suggest that this foraging tactic is socially learned and not an incidental event.

Another equally dramatic behavior, called “golden trevally hunting,” thus far has primarily been observed in one female dolphin named Wedges. Golden trevally (*Gnathanodon speciosus*) are a large schooling fish with a wide distribution in tropical and subtropical waters of the Indian and Pacific Oceans, including Shark Bay. Although feeding on juvenile golden trevally is common in Shark Bay, Wedges hunts the largest adults (reaching up to 1.2 m). Only Wedges has been directly observed catching large golden trevally, which entails prolonged chasing in deep water (>7 m) with dozens of high leaps to catch the fish, taking the fish down to the substrate, possibly to snap its neck, and finally, travelling to shallow water (<2 m) to break the fish into smaller piece using the substrate, all of which often takes over an hour (Mann & Sargeant, 2003). Although dolphins regularly break up large shallow water fishes on the seafloor, to date no dolphin other than Wedges has been observed catching deep-water fishes and bringing them to shallow water for processing. We have observed dolphins catching large snapper (Sparidae) in deep water on numerous occasions, but here dolphins spend considerable time and effort repeatedly diving to the deep bottom (>7 m) to break up the fish. Some of Wedges’ associates from the Puck family appear to have adopted her method as they have also been observed breaking up golden trevally in shallow water. However, only Wedges appears to specialize in the behavior, catching golden trevally every 2.6 h (Mann & Sargeant, 2003), whereas members of the Puck family, who have been followed intensively, have only been seen with trevally a few times.

Another intriguing behavior we call “shag robbing.” In Shark Bay, pied cormorants (*Phalacrocorax varius*), often called shags, regularly interact with dolphins, typically by stealing prey that dolphins ferret from the seafloor. Sometimes, dolphins try to get their prey back, but a young female named Sequel once reversed the roles of this “hunter–thief” relationship by instead, robbing the shags of their prey. After riding the bow wave of our boat, Sequel darted off in the direction of a shag more than 40 m away that was swallowing a fish. Almost as

soon as Sequel was out of sight she goosed the shags' underbelly, causing it startle, fly off, and drop the fish that she then quickly consumed. During the next 20 min of observation, she "robbed" a total of three different shags separated by hundreds of meters (JM & EMP, personal observation). What is so striking about this behavior is that Shark Bay dolphins virtually never steal prey from each other (Mann et al., 2007), making this technique novel in more ways than one.

Social and Sexual Behavior

While social living is thought to promote the occurrence and spread of all innovative behavior, it presents specific challenges that may elicit innovations with a social function. Earlier we described one social challenge solved by signature whistles and dialects: identifying preferred associates. However, nonvocal social innovations can also be used for this purpose. When two pods of southern resident killer whales meet, they perform a type of "greeting ceremony" in which the two pods first line up across from each other, then slowly begin their approach, and finally halt and pause before making physical contact (Osborne, 1986). After a brief moment, the whales submerge and form tight mixed groups and often engage in social and sexual behavior (Baird, 2000; Osborne, 1986). While the exact function of these ceremonies is unknown, it may be a form of cultural greeting, innovated within the southern resident clan. The northern residents too have their own unique tradition termed "beach rubbing" (Ford, 1989). Near Johnstone Strait, off Vancouver Island northern resident killer whales frequently visit one of several shallow beaches to rub on smooth pebbles. Although this was initially suggested to be a scratching exercise and may help to remove ectoparasites (Thomas, 1970), given that it usually occurs in groups and in conjunction with resting and social behavior, some have proposed a social function (Ford, 1989; Ford, Ellis, & Balcomb, 2000).

Among other delphinids, social innovation is less group specific and more widespread. For example, male bottlenose dolphins in Shark Bay, Australia perform elaborate physical displays, individually and synchronously, when in the presence of adult females (Connor, Smolker, & Richards, 1992a, 1992b). A variety of displays have been observed, including "rooster struts" (Figure 4.3) and "butterfly" displays, some of which are more common than others (Connor et al., 2000). Males vary considerably in their display repertoire and many displays have only ever been observed once (Connor et al., 2000; JM & EMP, personal observation) suggesting that males are flexible in their display behavior and regularly create novel displays. While the exact function of these



FIGURE 4.3 A male dolphin named Enchilada Starlet performing a display called a rooster strut in Shark Bay, Australia. *Photo taken by Janet Mann.*

displays is still unknown, the complexity, novelty, and synchrony of displays may advertise sexually selected characteristics (Trivers, 1972). In fact, such a hypothesis has been put forth regarding similar innovative display behavior performed by Amazon River dolphins, where males appear to manipulate sticks, grass, and clay to attract females (Martin, da Silva, & Rothery, 2008). From Herman and colleagues' work using the *tandem + create* command we know that bottlenose dolphins are certainly capable of inventing synchronous displays, and Kuczaj and colleagues' have demonstrated that males may vary in their ability to do so. Thus, if females exercise some mate choice based on the novelty of a male's display, innovative behavior in this species, as has been suggested for some spiders (Elias, 2006), could potentially be under sexual selection. Alternatively, or in addition, displays may have an agonistic or affiliative function that could be directed at females, males, or both (Connor et al., 2000). Irrespective of the function of male displays, they provide an impressive example of bottlenose dolphin innovative and creative behavior.

Another example of potential innovative social and sexual behavior comes from the vocalizations of some mysticetes, humpback whales being the best studied. Payne and McVay (1971) were perhaps the first to formally describe this behavior, which they call "singing." From recordings taken off the coast of Bermuda in the 1950s and 1960s, they noticed that humpbacks "produce a series of beautiful and varied sounds for a period of 7–30 min and then repeat the same series with considerable precision" (p. 597). Similar but simpler songs have now also been reported in bowhead whales, blue whales (*Balaenoptera*

musculus), fin whales (*Balaenoptera physalus*), and minke whales (Darling, 2009). At the time of Payne and McVay's recordings, very little was known concerning the function of these "sonorous moans and screams" (Schevill, 1964), and while this remains largely the case, we have learned a great deal about the context of singing. To date, all singers are male, and while song has been recorded during summer and winter near the poles (Garland et al., 2013; Magnúsdóttir, Rasmussen, Lammers, & Svavarsson, 2014), most singing occurs in warm, low latitude waters during the breeding season (Darling, 2009). As such, many suggest that song functions in reproduction. For example, it may act as a display or secondary sexual characteristic (Tyack, 1981), and given that males seem to congregate when singing, some suggest a lekking function (Clapham, 1996). It could serve to attract females (Tyack, 1981) and/or to signal status to other males (Darling & Bérubé, 2001). Others have proposed singing could help synchronize estrus between females, provide a way for males to appropriately space themselves on the breeding grounds, or even assist males in finding females by acting as a type of sonar (Darling, 2009). At the very least, singing seems to signal where males are and that breeding is underway.

While generally speaking all males in the same assemblage sing the same song at any one time (Payne & Guinee, 1983), over time this song changes in what might be considered innovation. Long-term studies have documented a gradual change in the songs of several populations of humpbacks (Garland et al., 2011; Noad, Cato, Bryden, Jenner, & Jenner, 2000; Payne & Payne, 1985), with some songs being completely replaced within only a few years (Noad et al., 2000). These changes, which include new sounds and/or the loss of old sounds, appear to occur during the winter breeding season and rapidly spread throughout an assemblage, presumably through social learning (Darling, 2009). Through time, song changes in one assemblage may also be transmitted to another. For example, Garland et al. (2011) recently documented the rapid spread of song types from eastern to western breeding populations in the South Pacific, in what they suggest was large scale horizontal social transmission. One song called the black song, which was first recorded in Western Australia in 1995, spread to Polynesia by 2001. In the northern hemisphere, similar transmission of songs may occur with recent findings suggesting a negative correlation between geographic proximity and assemblage song similarity (Darling, Acebes, & Yamaguchi, 2014). Exactly how these song variants get from one population to another is unclear. Low-level interchange between populations has been recorded suggesting that some males may physical carry songs from one group of whales to another. However, recent recordings of singing from the Antarctic, suggest that males from different populations could exchange songs during the summer while at their common

feeding grounds (Garland et al., 2013). As with killer whale and sperm whale dialects, humpback song may have some function, but whether a modification to a song alters its function, and thus is an innovation, is unclear. Given the current evidence, we cannot rule out that changes in both songs and dialects are nonfunctional and simply the result of errors in vocal copying and learning. In fact, this somewhat simpler explanation seems to be the case for many changes in the songs of passerine bird (Slater & Lachlan, 2003).

CETACEANS' INNOVATION ABILITIES

Given the intriguing novel, unique, and atypical behaviors described for both captive and wild cetaceans thus far, what can we conclude about their innovative and creative abilities? While most of the innovative and creative behavior performed by wild cetacea probably goes unobserved, odontocetes appear to innovate across a great breadth of functional domains including play, vocal communication, foraging, and social and sexual behavior. This may indicate that their ability to innovate, as has been suggested for humans, is domain general and underpinned by a single cognitive capacity, adaptable to a variety of contexts (Hauser, 2003). Such a view is supported by data indicating that at least in bottlenose dolphins, other related cognitive processes like imitation, are also domain general (Herman, 2012b). A similar argument has been recently made regarding primate cognition and intelligence (Reader, Hager, & Laland, 2011). Primate and odontocete societies share many characteristics (Yamagiwa & Karczmarski, 2014), which some believe helps explain their convergent cognitive abilities (Marino, 2002). In some primates, cognitive abilities appear to have coevolved across functional domains leading Reader et al. (2011) to suggest that some form of flexible, general intelligence was selected for in these species. Given that some odontocetes excel in a variety of cognition abilities (Herman, 2010), their innovative and creative skills could be an extension of a similar general intelligence. However, much greater detail on the cognitive abilities of a wider range of odontocete taxa are needed to better test this hypothesis.

Much less can be concluded regarding innovation and creativity in mysticetes. The understandable lack of captive studies is partly to blame, but with their expansive ranges and long dives, free-ranging mysticetes are often more difficult to study than odontocetes. Nonetheless, mysticetes show innovation in both play and foraging, and perhaps social and sexual behavior depending on how one interprets the data on humpback whale song. However, beyond simply documenting their ability to be innovative and perhaps creative, there is little we can say given the paucity of data.

What is somewhat clear is that examples for mysticetes are fewer and less diverse compared to odontocetes, for which there are several explanations. This discrepancy could reflect merely differences in research effort and ease of observation, or real differences in the taxa's innovative and creative abilities. For instance, it could be that being smaller, more agile, and having more maneuverable appendages and beaks, odontocetes simply have more manipulative ability than mysticetes. Greater manipulative ability increases the diversity of ways in which an organism can interact with its environment (both ecological and social) and thus we might expect the most manipulative of animals to show the greatest diversity in object manipulation. Whether or not manipulative ability and innovation/creativity are related remains to be seen, but such a hypothesis may be testable using data from primates and birds. Odontocetes and mysticetes also differ in their life history and ecology. First, while both suborders experience maternal care, odontocetes have a relatively longer period of maternal dependency (Whitehead & Mann, 2000), a feature thought to promote innovate and creative behavior. Second, many odontocetes live in relatively shallow water, near shore in a dynamic, diverse, and complex habitat, very different to that of most mysticetes. Of particular importance here may be the increase in ecological complexity (Sol, 2003) and availability of objects for manipulation (Mann & Patterson, 2013). In contrast, mysticetes, living primarily in deep-open water, may experience greater environmental stability and less complexity. Like many pelagic animals, mysticetes likely interact with few objects other than prey and conspecifics, and thus, may simply have little opportunity to be innovative or creative.

Combined, these examples from mysticetes and odontocetes provide much needed comparative data on animal innovation and creativity. Yet, many of these data are anecdotal and rarely discussed within the context of innovation and creativity. As such, we suggest that future cetacean researchers, particularly those studying wild populations, should (i) document in detail potential innovative and creative behavior, (ii) monitor the spread of such behaviors when possible, and (iii) place their data within a comparative framework to inform our understanding of the evolution of animal innovation and creativity.

COMPARATIVE INSIGHTS

While rigorous studies on animal innovation and creativity are still relatively recent, comparative data have provided information on both *who* innovates (among and within species) and *why* (proximate and ultimate causes). In regards to *who*, within species the literature is currently mixed. Some suggest that younger individuals are more likely to

innovate given that they are actively learning about their environment, often under the protection of kin (Kummer & Goodall, 1985; Lee, 2003). Yet others suggest that having fully developed their physical and cognitive skills, adults are the most likely to innovate (Reader & Laland, 2001). Evidence is also mixed regarding the sexes proclivity to innovate, but this discrepancy may be largely due to differences in reproductive interests and the context in which innovation occurs (i.e., females would be expected to be more innovative in foraging, and males in social behavior that provides access to mates) (Box, 2003; Laland & Bergen, 2003; Lee, 2003; Reader & Laland, 2001; Trivers, 1972). For social species, some evidence indicates social status may also affect innovative behavior with lower ranking chimpanzees (*Pan troglodytes*) innovating more than their higher-ranking conspecifics (Reader & Laland, 2001).

In captive cetaceans, many of the innovation examples, particularly those that occur in play, occur in younger individuals. For example, Kuczaj et al. (2006) found that approximately 80% of novel play behaviors observed in captivity were performed by calves and suggested that younger individuals may be an important source of behavioral variation and innovation (Kuczaj & Walker, 2006; Kuczaj et al., 2006). McBride and Hebb (1948) also note that younger individuals appear more playful and engage in more novel behavior. Yet these observations are not surprising since captive animals have plenty of time for play, and in younger individuals such behavior likely promotes both cognitive and physical development. What matters is if these behaviors are functional, transmit throughout the population, and are important for a species ecology and evolution, and for this we must turn to wild cetaceans. Unfortunately, here we rarely know the age of the innovator or even its species social system well enough to know if social status might matter. That said, data from wild cetaceans do suggest there may be sex differences in cetacean innovation, perhaps the most informative of which come from the Shark Bay. In Shark Bay, female bottlenose dolphins engage in a wide diversity of foraging tactics (e.g., Figure 4.2), many of which are likely innovations, while males perform extravagant novel social displays, some of which have only ever been observed once (e.g., Figure 4.3). Here, both sexes may be equally innovative and creative but the context in which they use these skills seems to reflect differences in fitness limiting factors: for female, access to food, and for males, access to mates. A similar situation may occur with male humpback whale song and male Amazon River dolphin displays, although in these species it is unclear if one sex is more innovative than the other in foraging behavior.

To address *why* animals might innovate or be creative it is helpful to first examine some of the possible consequences or benefits of

innovation. In other words, what does being innovative and creative allow a species or individual to do? Based on data primarily from birds and primates, Sol (2003) proposed several potential consequences of innovative and creative behavior. First, the ability to innovate is predicted to increase a species niche width (Sol, 2003). Within cetaceans, there may be some support for this predication as both killer whales and bottlenose dolphins, two of perhaps the most innovative and creative species, consume a wide variety of prey using a diverse set of innovative foraging tactics (Riesch et al., 2012; Sargeant & Mann, 2009). As such, these two species occupy a wide niche, but individual bottlenose dolphins and killer whales often utilize a much narrow niche, sometime associated with a particular innovation (Foote et al., 2013; Krützen et al., 2014; Patterson & Mann, 2011). Innovative species are also expected to have broad distributions (Sol, 2003). Again, as a species bottlenose dolphins and killer whales occupy a wide variety of habitats all over the world, but individually, dolphins and killer whales may have restricted ranges and even show habitat specialization (Riesch et al., 2012; Patterson, 2012). Such data are indicative of the taxa's great behavioral flexibility, which some suggest may be the result of their cognitive abilities. Indeed Herman (2006) suggests that it is bottlenose dolphins' cognitive abilities that may have lead to their widespread distribution and colonization of a great diversity of habitats. Such a hypothesis is consistent with data from birds and other mammals suggesting that increased cognitive ability positively correlate with a species ability to invade and colonize new habitats (Lefebvre & Bolhuis, 2003; Sol, Bacher, Reader & Lefebvre, 2008), although this may not universally be the case (Jönsson, Fabre, & Irestedt, 2012; Reader & MacDonald, 2003). Innovative species are also predicted to exhibit less migratory behavior (Sol, 2003), the idea being that species that are inflexible in their foraging must migrate to meet their energetic demands. The discrepancy between odontocete and mysticete innovation could provide preliminary support for this idea as nearly all mysticetes migrate, and most odontocetes do not (Lockyer & Brown, 1981), but we emphasize caution in this interpretation due to the sampling biases and difficulties of studying mysticetes mentioned above. The ability to innovate is also predicted to reduce susceptibility to extinction and lead to faster rates of evolution (Lefebvre & Bolhuis, 2003; Nicolakakis, Sol, & Lefebvre, 2003; Sol, 2003; Wyles, Kunkel, & Wilson, 1983). Many of the foraging innovations described above involve individuals adapting to increased anthropogenic threats, which could provide support for first of these claims, but if this will ultimately increase species' resistance to extinction is unknown. Data from killer whales may support the second claim given that maternally transmitted foraging innovations may be leading to speciation (Riesch et al., 2012). Yet, the

relationship between innovation and evolution could go either way depending on ecological stability. As with learning (Stephens, 1991), if an innovation is consistently adaptive between generations, we might expect it to become fixed and encoded genetically, and if this somehow leads to reproductive isolation, this could result in speciation. However, if there is some ecological instability between generations, behavioral flexibility, and thus the *ability* to be innovative, might be favored which would not increase the rate of evolution. After all, innovative species are flexible by definition and it may be this behavioral plasticity, rather than some specific, innovation that is most adaptive.

Having reviewed some of the benefits, we can hypothesize as to possible driving forces behind the selection of innovation and creativity, or whether or not it is selected for at all. It is important to note that simply because an innovation may appear to provide some benefit, say allowing for an increase in niche width, it does not necessarily follow that this benefit was driving force behind ones innovative abilities (Gould & Lewontin, 1979). Being innovative and creative likely has many benefits across a wide range of social, ecological, and evolutionary contexts so it is likely that multiple forces are at work. Two key functional domains that may favor innovation and creativity are resource acquisition (foraging) and courtship or mating (sexual). For example, innovations in foraging behavior and diet may reduce intraspecific competition, which could ultimately allow for increased population density. Support for this comes from the Shark Bay dolphins who have one of the highest population densities reported for bottlenose dolphins (Watson-Capps, 2005) and may also exhibit the greatest diversity in foraging behavior. While we know of no clear link between foraging innovations and population density in killer whales, some of their innovative behavior may actually be in response to interspecific competition with humans (Estes et al., 1998). Since foraging pressures are perhaps greatest on females due to the increased reproductive demands, it would not be surprising if natural selection favored foraging innovation in females. Sexual selection on the other hand may select for innovative and creative behavior in males, particularly in the context of displays used to attract mates. Among cetaceans, male odontocete displays and mysticete song may be an example of such sexually selected innovative and creative behavior. Outside of cetaceans, one of the best examples of sexually selected innovation comes from male satin bowerbirds (*Ptilonorhynchus violaceus*) that selectively decorate their bowers to increase its uniqueness and novelty (Borgia, Kaatz, & Condit, 1987). Thus, as has been argued for in humans (Simonton, 2003), both sexual and natural selection seems to favor innovative and creative behavior in some animals species, the extent to which we are only beginning to understand.

References

- Alexander, R. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325–383.
- Allen, J., Weinrich, M. T., Hoppitt, W., & Rendell, L. E. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340, 485–488.
- Allen, S. J., Bejder, L., & Krützen, M. (2011). Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? *Marine Mammal Science*, 27, 449–454.
- Ashford, J., Rubilar, P., & Martin, A. R. (1996). Interactions between cetaceans and longline fishery operations around South Georgia. *Marine Mammal Science*, 12, 452–457.
- Baird, R. W. (2000). The killer whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies, field studies of dolphins and whales* (pp. 127–154). Chicago, IL: The University of Chicago Press.
- Baird, R. W. (2002). *Killer whales of the world: Natural history and conservation*. Stillwater, MN: Voyageur Press.
- Barrett-Lennard, L.G. (2000). Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis (Ph.D. thesis) (p. 97). Vancouver, Canada: Department of Zoology, University of British Columbia.
- Bateson, P., & Martin, P. (2013). *Play, playfulness, creativity and innovation*. Cambridge, UK: Cambridge University Press.
- Beckoff, M., & Byers, J. A. (1981). A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: An ethological hornet's nest. In M. Main, K. Immelmann, G. W. Barlow, & L. Petrinovich (Eds.), *Behavioral development: The bielefeld interdisciplinary project* (pp. 296–337). Cambridge, UK: Cambridge University Press.
- Beckoff, M., & Byers, J. A. (1998). *Animal play: Evolutionary, comparative and ecological perspectives*. Cambridge, UK: Cambridge University Press.
- Birtles, A., & Mangott, A. (2013). Highly interactive behaviour of inquisitive dwarf minke whales. In *Whales and dolphins: cognition, culture, conservation and human perceptions* (pp. 140–148). New York, NY: Routledge.
- Bloch, D., & Lockyer, C. H. (1988). Killer whales (*Orcinus orca*) in Faroese waters. *Rit Fiskideildar*, 11, 55–64.
- Borgia, G., Kaatz, I., & Condit, R. (1987). Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus violaceus*: A test of hypotheses for the evolution of male display. *Animal Behaviour*, 35, 1129–1139.
- Box, H. O. (2003). Characteristics and propensities of marmosets and tamarins: Implications for studies of innovation. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 197–222). Oxford, UK: Oxford University Press.
- Brady, E. J. (1909). The law of the tongue: Whaling by compact at Twofold Bay. *Australia To-Day*, 37–39.
- Braslau-Schneck, S. (1994). Innovative behaviors and synchronization in bottlenose dolphins (MA thesis). Honolulu, HI: Department of Psychology, University of Hawaii.
- Brown, D., & Norris, K. (1956). Observations of captive and wild cetaceans. *Journal of Mammalogy*, 37, 311–326.
- Bruck, J. N. (2013). Decades-long social memory in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131726.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature*, 207, 434–435.
- Caldwell, M. C., & Caldwell, D. K. (1968). Vocalization of naive captive dolphins in small groups. *Science*, 159, 1121–1123.

- Caldwell, M. C., & Caldwell, D. K. (1971). Statistical evidence for individual signature whistles in Pacific white-sided dolphins, *Lagenorhynchus obliquidens*. *Cetology*, 3, 1–9.
- Caldwell, M. C., & Caldwell, D. K. (1979). The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*)—ontogeny. In H. E. Winn, & B. L. Olla (Eds.), *Behavior of marine animals: Current perspectives in research. Volume 3: Cetaceans* (pp. 369–401). New York, NY: Plenum Press.
- Caldwell, M. C., Caldwell, D. K., & Miller, J. F. (1973). Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon*. *Cetology*, 16, 1–21.
- Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood, & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 199–234). San Diego, CA: Academic Press.
- Chilvers, B. L., & Corkeron, P. J. (2001). Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society B: Biological Sciences*, 268, 1901–1905.
- Chivers, S. J. (2009). Cetacean life history. In W. F. Perrin, B. Würsig, & J. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 215–220). Burlington, MA: Academic Press.
- Clapham, P. J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. *Mammal Review*, 26, 27–49.
- Clapham, P. J. (2000). The humpback whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies, field studies of dolphins and whales* (pp. 173–196). Chicago, IL: The University of Chicago Press.
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992a). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, 89, 987–990.
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992b). Dolphin alliances and coalitions. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415–443). Oxford, UK: Oxford University Press.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission–fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies, field studies of dolphins and whales* (pp. 91–125). Chicago, IL: University of Chicago Press.
- Cook, M. L. H., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2004). Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B: Biological Sciences*, 271, 1043–1049.
- Corkeron, P. J. (2009). Captivity. In W. F. Perrin, B. Würsig, & J. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 183–188). Burlington, MA: Academic Press.
- Couch, L. (1930). Humpback whale killed in Puget Sound, Washington. *The Murrelet*, 11, 75.
- Dahlheim, M. E., & White, P. A. (2010). Ecological aspects of transient killer whales *Orcinus orca* as predators in southeastern Alaska. *Wildlife Biology*, 16, 308–322.
- Dahlheim, M. E., Schulman-Janiger, A., Black, N., Ternullo, R., Ellifrit, D., & Balcomb, K. C., III (2008). Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): Occurrence, movements, and insights into feeding ecology. *Marine Mammal Science*, 24, 719–729.
- Dakin, W. J. (1934). *Whalemen adventures: the story of whaling in Australian waters and other southern seas related thereto, from the days of sails to modern times* (1st ed.). Sydney, Australia: Angus and Robertson.
- Darling, J. D., & Bérubé, M. (2001). Interactions of singing humpback whales with other males. *Marine Mammal Science*, 17, 570–584.
- Darling, J. D. (2009). Song. In W. F. Perrin, B. Würsig, & J. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 1053–1056). Burlington, MA: Academic Press.
- Darling, J. D., Acebes, J., & Yamaguchi, M. (2014). Similarity yet a range of differences between humpback whale songs recorded in the Philippines, Japan and Hawaii in 2006. *Aquatic Biology*, 21, 93–107.

- Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D., & Simões-Lopes, P. C. (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biology Letters*, *8*, 702–705.
- De Oliveira, C. R., Ruiz-Miranda, C. R., Kleiman, D. G., & Beck, B. B. (2003). Play behavior in juvenile golden lion tamarins (Callitrichidae: Primates): Organization in relation to costs. *Ethology*, *109*, 593–612.
- Deakos, M. H., Branstetter, B. K., Mazzuca, L., Fertl, D., & Mobley, J. R. (2010). Two unusual interactions between a bottlenose dolphin (*Tursiops truncatus*) and a humpback whale (*Megaptera novaeangliae*) in Hawaiian waters. *Aquatic Mammals*, *36*, 121–128.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, *60*, 629–638.
- Deecke, V. B., Nykänen, M., Foote, A., & Janik, V. M. (2011). Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology*, *13*, 79–88.
- Defran, R. H., & Pryor, K. W. (1980). The behavior and training of cetaceans in captivity. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 319–362). New York, NY: John Wiley & Sons.
- Delfour, F., & Aulagnier, S. (1997). Bubbleblow in beluga whales (*Delphinapterus leucas*): A play activity?. *Behavioural Processes*, *40*, 183–186.
- DeMaster, D. P., Trites, A. W., Clapham, P. J., Mizroch, S., Wade, P., Small, R. J., et al. (2006). The sequential megafaunal collapse hypothesis: Testing with existing data. *Progress in Oceanography*, *68*, 329–342.
- Donaldson, R., Finn, H., Bejder, L., Lusseau, D., & Calver, M. (2012). The social side of human–wildlife interaction: Wildlife can learn harmful behaviours from each other. *Animal Conservation*, *15*, 427–435.
- Dos Santos, M. E., & Lacerda, M. (1987). Preliminary observations of the bottlenose dolphin (*Tursiops truncatus*) in the Sado Estuary (Portugal). *Aquatic Mammals*, *13*, 65–80.
- Duarte de Figueiredo, L., & Simão, S. M. (2009). Possible occurrence of signature whistles in a population of *Sotalia guianensis* (Cetacea, Delphinidae) living in Sepetiba Bay, Brazil. *The Journal of the Acoustical Society of America*, *126*, 1563–1569.
- Duffy-Echevarria, E. E., Connor, R. C., & St. Aubin, D. J. (2008). Observations of strand-feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South Carolina. *Marine Mammal Science*, *24*, 202–206.
- Elias, D. O. (2006). Female preference for complex/novel signals in a spider. *Behavioral Ecology*, *17*, 765–771.
- Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, *282*, 473–476.
- Fearnbach, H., Durban, J. W., Ellifrit, D. K., Waite, J. M., Matkin, C. O., Lunsford, C. R., et al. (2013). Spatial and social connectivity of fish-eating “resident” killer whales (*Orcinus orca*) in the northern North Pacific. *Marine Biology*, *161*, 459–472.
- Fertl, D., & Würsig, B. (1995). Coordinated feeding by Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico. *Aquatic Mammals*, *21.1*, 3–5.
- Fisher, J., & Hinde, R. A. R. (1949). The opening of milk bottles by birds. *British Birds*, *42*, 347–357.
- Foote, A. D., Newton, J., Ávila-Arcos, M. C., Kampmann, M.-L., Samaniego, J. A., Post, K., et al. (2013). Tracking niche variation over millennial timescales in sympatric killer whale lineages. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131481.
- Foote, A. D., Newton, J., Piertney, S. B., Willerslev, E., & Gilbert, M. T. P. (2009). Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology*, *18*, 5207–5217.
- Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*, 727–745.

- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, 69, 1454–1483.
- Ford, J. K. B. (2008). Dialects. In W. F. Perrin, B. Würsig, & J. Thewissen (Eds.), *Encyclopædia of marine mammals* (2nd ed., pp. 310–311). Burlington, MA: Academic Press.
- Ford, J. K. B., & Ellis, G. M. (2014). You are what you eat: foraging specializations and their influence on the social organization and behaviour of killer whales. In J. Yamagiwa, & L. Karczmarski (Eds.), *Primates and cetaceans: Field research and conservation of complex mammalian societies* (pp. 75–98). New York, NY: Springer.
- Ford, J. K. B., Ellis, G. M., & Balcomb, K. C. (2000). *Killer whales: The natural history and genealogy of Orca orcinus in British Columbia and Washington* (2nd ed.). Vancouver, BC: University of British Columbia Press.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., & Balcomb, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 1471, 1456–1471.
- Ford, J. K. B., Ellis, G. M., Matkin, C. O., Wetklo, M. H., Barrett-Lennard, L. G., & Withler, R. E. (2011). Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology*, 11, 213–224.
- Foroughirad, V., & Mann, J. (2013). Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biological Conservation*, 160, 242–249.
- Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A. D., Buckstaff, K., Jankowski, K., et al. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, 8, 17–26.
- Gagliano, M., Renton, M., Depczynski, M., & Mancuso, S. (2014). Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia*, 175, 63–72.
- Garland, E. C., Gedamke, J., Rekdahl, M. L., Noad, M. J., Garrigue, C., & Gales, N. (2013). Humpback whale song on the Southern Ocean feeding grounds: Implications for cultural transmission. *PLoS One*, 8, e79422.
- Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., et al. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, 21, 687–691.
- Gewalt, W. (1989). Orinoco-freshwater-dolphins (*Inia geoffrensis*) using self-produced air bubble “rings” as toys. *Aquatic Mammals*, 15, 73–79.
- Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, 76, 375–387.
- Gilmore, R. M. (1976). The friendly whales of Laguna San Ignacio. *Terra*, 15, 24–28.
- Gonzalvo, J., Valls, M., Cardona, L., & Aguilar, A. (2008). Factors determining the interaction between common bottlenose dolphins and bottom trawlers off the Balearic Archipelago (western Mediterranean Sea). *Journal of Experimental Marine Biology and Ecology*, 367, 47–52.
- Gould, S., & Lewontin, R. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society B: Biological Sciences*, 204, 581–598.
- Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation*. Oxford, UK: Oxford University Press.
- Gridley, T., Cockcroft, V. G., Hawkins, E. R., Blewitt, M. L., Morisaka, T., & Janik, V. M. (2013). Signature whistles in free-ranging populations of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*. *Marine Mammal Science*, 30, 512–527.

- Groos, K., Baldwin, E. L., & Baldwin, J. M. (1898). *The play of animals*. New York, NY: Appleton.
- Guinet, C. (1991). Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology*, *69*, 2712–2716.
- Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, *73*, 27–33.
- Hain, J. H. W., Carter, G. R., Kraus, S. D., Mayo, C. A., & Winn, H. E. (1982). Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin*, *80*, 259–268.
- Hamer, D. J., Childerhouse, S. J., & Gales, N. J. (2012). Odontocete bycatch and depredation in longline fisheries: A review of available literature and of potential solutions. *Marine Mammal Science*, *28*, E345–E374.
- Hauser, M. D. (2003). To innovate or not to innovate? That is the question. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 329–338). Oxford, UK: Oxford University Press.
- Herman, D. P., Burrows, D. G., Wade, P. R., Durban, J. W., Matkin, C. O., Leduc, R. G., et al. (2005). Feeding ecology of eastern Northern Pacific killer whales *Orcinus orca* from fatty acid, stable isotope and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series*, *302*, 275–291.
- Herman, L. M. (1991). What the dolphin knows, or might know, in its natural world. In K. Pryor, & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 349–364). Berkeley, CA: University of California Press.
- Herman, L. M. (2002). Vocal, social, and self imitation by bottlenosed dolphins. In K. Dautenhahn, & C. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 63–108). Cambridge, MA: MIT Press.
- Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley, & M. Nudds (Eds.), *Rational animals?* (pp. 437–468). Oxford: Oxford University Press.
- Herman, L. M. (2010). What laboratory research has told us about dolphin cognition. *International Journal of Comparative Psychology*, *23*, 310–330.
- Herman, L. M. (2012a). Historical perspectives: Birthing a dolphin research laboratory: The early history of the Kewalo Basin Marine Mammal Laboratory. *Aquatic Mammals*, *38*, 102–125.
- Herman, L. M. (2012b). Body and self in dolphins. *Consciousness and Cognition*, *21*, 526–545.
- Heubeck, M. (2001). Pilot whale apparently playing with moulting common eiders. *Scottish Birds*, *22*, 62.
- Hewitt, O. (1986). Dolphin interferes with loon. *Florida Field Naturalist*, *14*, 100.
- Hoelzel, A. R. (1991). Killer whale predation on marine mammals at Punta Norte, Argentina; Food sharing, provisioning and foraging strategy. *Behavioral Ecology and Sociobiology*, *29*, 197–204.
- Hoese, H. (1971). Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy*, *52*, 222–223.
- Holmes, B., & Neil, D. (2012). “Gift giving” by wild bottlenose dolphins (*Tursiops* sp.) to humans at a wild dolphin provisioning program, Tangalooma, Australia. *Anthrozoos*, *25*, 397–413.
- Holth, P. (2012). The creative porpoise revisited. *European Journal of Behavior Analysis*, *1*, 1–5.
- Huang, P., Sieving, K. E., & Mary, C. M. S. (2011). Heterospecific information about predation risk influences exploratory behavior. *Behavioral Ecology*, *23*, 463–472.
- Ingebrigtsen, A. (1929). Whales caught in the North Atlantic and other seas.. *International Council for the Exploration of the Sea. Rapports et Proces-Verbaux des Reunions*, *56*, 1–26.

- Janik, V. M., & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 199, 479–489.
- Janik, V. M., & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, 56, 829–838.
- Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. *Wildlife Monographs*, 144, 1–65.
- Jefferson, T. A., Stacey, P., & Baird, R. W. (1991). A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review*, 21, 151–180.
- Johnson, C. M., & Norris, K. S. (1994). Social behavior. In *The Hawaiian spinner dolphin* (pp. 243–286). Berkeley, CA: The University of California Press.
- Jones, I. (2006). A northeast Pacific offshore killer whale (*Orcinus orca*) feeding on a Pacific halibut (*Hippoglossus stenolepis*). *Marine Mammal Science*, 22, 198–200.
- Jones, M. L., & Swartz, S. L. (1984). Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In M. L. Jones, & S. L. Swartz (Eds.), *The gray whale: Eschrichtius robustus* (Vol. 1, pp. 309–374). Orlando, FL: Academic Press.
- Jönsson, K. A., Fabre, P.-H., & Irestedt, M. (2012). Brains, tools, innovation and biogeography in crows and ravens. *BMC Evolutionary Biology*, 12, 1–12.
- Jurasz, C. M., & Jurasz, V. P. (1979). Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Scientific Reports of the Whales Research Institute*, 31, 69–83.
- Kasuya, T., & Marsh, H. (1984). Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Report of the International Whaling Commission*, 6, 259–310.
- Kaufman, A. B., Butt, A. E., Kaufman, J. C., & Colbert-White, E. N. (2011). Towards a neurobiology of creativity in nonhuman animals. *Journal of Comparative Psychology*, 125, 255–272.
- Kaufman, J. C., & Kaufman, A. B. (2004). Applying a creativity framework to animal cognition. *New Ideas in Psychology*, 22, 143–155.
- Kemper, C. M., Pemberton, D., Cawthorn, M., Heinrich, S., Mann, J., Würsig, B., et al. (2003). Aquaculture and marine mammals: Coexistence or conflict? In N. Gales, M. Hindell, & R. Kirkwood (Eds.), *Marine mammals: Fisheries, tourism and management issues* (pp. 208–228). Collingwood, Australia: CSIRO Publishing.
- King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 13216–13221.
- King, S. L., Sayigh, L. S., Wells, R. S., Fellner, W., & Janik, V. M. (2013). Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130053.
- Kopps, A. M., Ackermann, C. Y., Sherwin, W. B., Allen, S. J., Bejder, L., & Krützen, M. (2014). Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 281, 2013245.
- Kopps, A. M., Krützen, M., Allen, S. J., Bacher, K., & Sherwin, W. B. (2013). Characterizing the socially transmitted foraging tactic “sponging” by bottlenose dolphins (*Tursiops* sp.) in the western gulf of Shark Bay, Western Australia. *Marine Mammal Science*, 30, 847–863.
- Krahn, M. M., Herman, D. P., Matkin, C. O., Durban, J. W., Barrett-Lennard, L. G., Burrows, D. G., et al. (2007). Use of chemical tracers in assessing the diet and foraging regions of eastern North Pacific killer whales. *Marine Environmental Research*, 63, 91–114.

- Kritzler, H. (1952). Observations on the pilot whale in captivity. *Journal of Mammalogy*, *33*, 321–334.
- Krützen, M., Kreicker, S., MacLeod, C. D., Learmonth, J., Kopps, A. M., Walsham, P., et al. (2014). Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20140374.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 8939–8943.
- Kuczaj, S. A., & Eskelinen, H. C. (2014). The “creative dolphin” revisited: what do dolphins do when asked to vary their behavior? *Animal Behavior and Cognition*, *1*, 66–76.
- Kuczaj, S. A., Lacinak, C. T., Garver, A., & Scarpuzzi, M. (1998). Can animals enrich their own environment? In V. J. Hare, & K. E. Worley (Eds.), *Proceedings of the third international conference on environmental enrichment* (pp. 168–170). Orlando, FL: The Shape of Enrichment, Inc.
- Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology*, *19*, 223–240.
- Kuczaj, S. A., & Walker, R. T. (2006). How do dolphins solve problems? In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative Cognition: Experimental Explorations of Animal Intelligence* (pp. 580–601). New York, NY: Oxford University.
- Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *308*, 203–214.
- Laland, K. N., & Bergen, Y. Van (2003). Experimental studies of innovation in the guppy. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 155–174). Oxford, UK: Oxford University Press.
- Leatherwood, S. (1975). Some observations of feeding behavior of bottle-nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. *Marine Fisheries Review*, *37*, 10–16.
- Lee, P. C. (2003). Innovation as a behavioural response to environmental challenges: A cost and benefit approach. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 261–268). Oxford, UK: Oxford University Press.
- Lefebvre, L., & Bolhuis, J. J. (2003). Positive and negative correlations of feeding innovations in birds: Evidence for limited modularity. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 39–62). Oxford, UK: Oxford University Press.
- Lefebvre, L., Reader, S. M., & Sol, D. (2013). Innovating innovation rate and its relationship with brains, ecology and general intelligence. *Brain, Behavior and Evolution*, *81*, 143–145.
- Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour*, *53*, 549–560.
- Lewis, J. S., & Schroeder, W. W. (2003). Mud plume feeding, a unique foraging behavior of the bottlenose dolphin (*Tursiops truncatus*) in the Florida Keys. *Gulf of Mexico Science*, *21*, 92–97.
- Lockyer, C. H., & Brown, S. G. (1981). The migration of whales. In D. J. Aidley (Ed.), *Animal migration* (Issue 13., pp. 105–137). Cambridge, UK: Cambridge University Press.
- Lopez, J., & Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. *Journal of Mammalogy*, *66*, 181–183.
- Loughlin, T. R. (Ed.), (1994). *Marine mammals and the Exxon Valdez*. New York, NY: Academic Press.

- Lyrholm, T., Leimar, O., Johannesson, B., & Gyllenstein, U. (1999). Sex-biased dispersal in sperm whales: Contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal Society B: Biological Sciences*, 266, 347–354.
- Magnúsdóttir, E. E., Rasmussen, M. H., Lammers, M. O., & Svavarsson, J. (2014). Humpback whale songs during winter in subarctic waters. *Polar Biology*, 37, 427–433.
- Manabe, K. (1997). Control of vocal repertoire by reward in budgerigars (*Melopsittacus undulatus*). *Journal of Comparative Psychology*, 111, 50–62.
- Manabe, K., & Dooling, R. J. (1997). Control of vocal production in budgerigars (*Melopsittacus undulatus*): Selective reinforcement, call differentiation, and stimulus control. *Behavioural Processes*, 41, 117–132.
- Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368, 20120424.
- Mann, J., & Sargeant, B. L. (2003). Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In D. Fragaszy, & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 236–266). Cambridge, UK: Cambridge University Press.
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, 136, 529–566.
- Mann, J., & Watson-Capps, J. J. (2005). Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp.. *Animal Behaviour*, 69, 899–909.
- Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, 11, 210–219.
- Mann, J., Sargeant, B. L., & Minor, M. (2007). Calf inspections of fish catches in bottlenose dolphins (*Tursiops* sp.): Opportunities for oblique social learning? *Marine Mammal Science*, 23, 197–202.
- Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C., et al. (2008). Why do dolphins carry sponges? *PLoS One*, 3, e3868.
- Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications*, 3, 980.
- Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution*, 59, 21–32.
- Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996). Ring bubbles of dolphins. *Scientific American*, 275, 82–87.
- Martin, A. R., da Silva, V. M. F., & Rothery, P. (2008). Object carrying as socio-sexual display in an aquatic mammal. *Biology Letters*, 4, 243–245.
- McBride, A., & Hebb, D. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. *Journal of Comparative and Physiological Psychology*, 41, 111–123.
- McCowan, B., & Reiss, D. (2001). The fallacy of “signature whistles” in bottlenose dolphins: A comparative perspective of “signature information” in animal vocalizations. *Animal Behaviour*, 62, 1151–1162.
- McCowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): Implications for cognition. *Journal of Comparative Psychology*, 114, 98–106.
- Mercado, E., Murray, S. O., Uneyama, R. K., Pack, A. A., & Herman, L. M. (1998). Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning & Behavior*, 26, 210–218.
- Mercado, E., Uneyama, R. K., Pack, A. A., & Herman, L. M. (1999). Memory for action events in the bottlenosed dolphin. *Animal Cognition*, 2, 17–25.

- Miller, P. (2002). Mixed-directionality of killer whale stereotyped calls: a direction of movement cue? *Behavioral Ecology and Sociobiology*, *52*, 262–270.
- Moller, A. P., & Garamszegi, L. Z. (2012). Between individual variation in risk-taking behavior and its life history consequences. *Behavioral Ecology*, *23*, 843–853.
- Nakahara, F., & Takemura, A. (1997). A survey on the behavior of captive odontocetes in Japan. *Aquatic Mammals*, *23.3*, 135–143.
- National Marine Fisheries Service Office of Protected Resources. (2014). *U.S. marine mammal inventory report*. Available at <<http://www.nmfs.noaa.gov/pr/permits/inventory.htm>>.
- Nicolakakis, N., Sol, D., & Lefebvre, L. (2003). Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, *65*, 445–452.
- Nishiwaki, M. (1962). Aerial photographs show sperm whales' interesting habits. *Norsk Hvalfangst-Tidende*, *51*, 395–398.
- Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., & Jenner, K. C. (2000). Cultural revolution in whale songs. *Nature*, *408*, 537–538.
- Noke, W., & Odell, D. (2002). Interactions between the Indian River Lagoon blue crab fishery and the bottlenose dolphin, *Tursiops truncatus*. *Marine Mammal Science*, *18*, 819–832.
- Nolan, C., Liddle, G., & Elliot, J. (2000). Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. *Marine Mammal Science*, *16*, 658–664.
- Noonan, M. (2005). Gull baiting in captive orcas: A possible instance of cultural transmission. In *Animal behavior society meeting, August 6–10*, Snowbird, UT.
- Nousek, A. E., Slater, P. J. B., Wang, C., & Miller, P. J. O. (2006). The influence of social affiliation on individual vocal signatures of northern resident killer whales (*Orcinus orca*). *Biology Letters*, *2*, 481–484.
- Oftedal, O. T. (1997). Lactation in whales and dolphins: Evidence of divergence between baleen- and toothed-species. *Journal of Mammary Gland Biology and Neoplasia*, *2*, 205–230.
- Olesiuk, P. F., Bigg, M., & Ellis, G. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters off British Columbia and Washington state. *Report of the International Whaling Commission*, *12*, 209–243.
- Orams, M. B. (2002). Feeding wildlife as a tourism attraction: A review of issues and impacts. *Tourism Management*, *23*, 281–293.
- Osborne, R. W. (1986). A behavioral budget of Puget Sound killer whales. In B. C. Kirkeveld, & J. S. Lockard (Eds.), *Behavioral biology of killer whales* (pp. 211–249). New York, NY: A. Liss.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. Oxford, UK: Oxford University Press.
- Patterson, E.M. (2012). Ecological and life history factors influence habitat and tool use in wild bottlenose dolphins (*Tursiops* sp.) (PhD thesis) (p. 170). Washington, DC, Georgetown: Department of Biology, Georgetown University.
- Patterson, E. M., & Mann, J. (2011). The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). *PLoS One*, *6*, e22243.
- Paulos, R., Trone, M., & Kuczaj, S. A. (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology*, *23*, 701–722.
- Payne, K., & Payne, R. S. (1985). Large scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie*, *68*, 89–114.
- Payne, R. S., & Guinee, L. N. (1983). Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks.". In R. S. Payne (Ed.), *Communication and behavior of whales* (AAAS Selec ed., pp. 333–358). Boulder, CO: Westview Press.
- Payne, R. S., & McVay, S. (1971). Songs of humpback whales. *Science*, *173*, 585–597.

- Peddemors, V. M., & Thompson, G. (1994). Beaching behaviour during shallow water feeding by humpback dolphins *Sousa plumbea*. *Aquatic Mammals*, 20, 65–76.
- Pennino, M. G., Mendoza, M., Pira, A., Floris, A., & Rotta, A. (2013). Assessing foraging tradition in wild bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 39, 282–289.
- Perrin, W.F. (2014). *World cetacea database*. <<http://www.marinespecies.org/cetacea>> Accessed 27.02.15.
- Pitman, R. L., & Durban, J. W. (2010). Killer whale predation on penguins in Antarctica. *Polar Biology*, 33, 1589–1594.
- Pitman, R. L., & Durban, J. W. J. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science*, 28, 16–36.
- Pitman, R. L., & Ensor, P. (2003). Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, 5, 131–139.
- Plucker, J. A., Beghetto, R. A., & Dow, G. T. (2004). Why isn't creativity more important to educational psychologists? Potentials, pitfalls, and future directions in creativity research. *Educational Psychologist*, 39, 83–96.
- Pryor, K. W. (2004a). *On behavior: Essays & research*. Waltham, MA: Sunshine Books, Inc..
- Pryor, K. W. (2004b). *Lads before the wind: Diary of a dolphin trainer* (4th ed.). Waltham, MA: Sunshine Books, Inc..
- Pryor, K. W. (2006). *Don't shoot the dog!: The new art of teaching and training* (3rd ed.). Lydney, UK: Ringpress Books Limited.
- Pryor, K. W. (2009). *Reaching the animal mind: Clicker training and what it teaches us about all animals*. New York, NY: Scribner.
- Pryor, K. W., Haag, R., & O'Reilly, J. (1969). The creative porpoise: Training for novel behavior. *Journal of the Experimental Analysis of Behavior*, 12, 653–661.
- Pryor, K. W., Lindbergh, J., Lindbergh, S., & Milano, R. (1990). A dolphin–human fishing cooperative in Brazil. *Marine Mammal Science*, 6, 77–82.
- Purves, M., Agnew, D., & Balguerias, E. (2004). Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) interactions with longline vessels in the Patagonian toothfish fishery at South Georgia, South Atlantic. *CCAMLR Science*, 11, 111–126.
- Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, 30, 393–432.
- Read, A. J. (2001). Trends in the maternal investment of harbour porpoises are uncoupled from the dynamics of their primary prey. *Proceedings of the Royal Society B: Biological Sciences*, 268, 573–577.
- Reader, S. M. (2003). Innovation and social learning: Individual variation and brain evolution. *Animal Biology*, 53, 147–158.
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, 22, 787–805.
- Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 4436–4441.
- Reader, S. M., & Laland, K. N. (2003). Animal innovation: an introduction. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 4–35). Oxford, UK: Oxford University Press.
- Reader, S. M., & MacDonald, K. (2003). Environmental variability and primate behavioral flexibility. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (p. 4). Oxford, UK: Oxford University Press.
- Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366, 1017–1027.

- Rendell, L. E., & Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society B: Biological Sciences*, 270, 225–231.
- Rendell, L. E., & Whitehead, H. (2005). Spatial and temporal variation in sperm whale coda vocalizations: Stable usage and local dialects. *Animal Behaviour*, 70, 191–198.
- Renjun, L., Gewalt, W., Neurohr, B., & Winkler, A. (1994). Comparative studies on the behaviour of *Inia geoffrensis* and *Lipotes vexillifer* in artificial environments. *Aquatic Mammals*, 20.1, 39–45.
- Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B., & Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: Ecological speciation in killer whales? *Biological Journal of the Linnean Society*, 106, 1–17.
- Rigley, L., VanDyke, V. G., Cram, P., & Rigley, I. (1981). Shallow water behavior of the Atlantic bottlenose dolphin (*Tursiops truncatus*). *Proceedings of the Pennsylvania Academia of Science*, 55, 157–159.
- Russon, A. E. (2003). Innovation and creativity in forest-living rehabilitant orang-utans. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 279–308). Oxford, UK: Oxford University Press.
- Samuels, A., & Bejder, L. (2004). Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida, USA. *Journal of Cetacean Research and Management*, 6, 69–77.
- Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour*, 78, 715–721.
- Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, 83, 1400–1410.
- Saulitis, E., Matkin, C., Barrett-Lennard, L. G., Heise, K., & Ellis, G. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, 16, 94–109.
- Sayigh, L. S., Quick, N., Hastie, G., & Tyack, P. L. (2013). Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*. *Marine Mammal Science*, 29, 312–324.
- Sayigh, L. S., Tyack, P. L., & Wells, R. (1995). Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, 36, 171–177.
- Sayigh, L. S., Tyack, P. L., Wells, R., & Scott, M. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother–offspring comparisons. *Behavioral Ecology and Sociobiology*, 26, 247–260.
- Schevill, W. E. (1964). Underwater sounds of cetaceans. In Tavo (Ed.), *Marine bioacoustics* (pp. 307–316). New York, NY: Pergamon.
- Schusterman, R. J., & Reichmuth, C. (2007). Novel sound production through contingency learning in the Pacific walrus (*Odobenus rosmarus divergens*). *Animal Cognition*, 11, 319–327.
- Shapiro, A. D. (2006). Preliminary evidence for signature vocalizations among free-ranging narwhals (*Monodon monoceros*). *The Journal of the Acoustical Society of America*, 120, 1695–1705.
- Sigurjónsson, J. (1988). Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar*, 11, 99–114.
- Silber, G. K., & Fertl, D. (1995). Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River Delta, Mexico. *Aquatic Mammals*, 21, 183–186.
- Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71, 1494–1499.
- Similä, T., Holst, J. C., & Christensen, I. (1996). Occurrence and diet of killer whales in northern Norway: Seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 769–779.

- Simões-Lopes, P. C., Fabián, M. E., & Menegheti, J. O. (1998). Dolphin interactions with the mullet artisanal fishing on southern Brazil: A qualitative and quantitative approach. *Revista Brasileira de Zoologia*, *15*, 709–726.
- Simonton, D. K. (2003). Human creativity: Two Darwinian analyses. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 309–328). Oxford, UK: Oxford University Press.
- Slater, P. J. B., & Lachlan, R. F. (2003). Is innovation in bird song adaptive? In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 117–136). Oxford, UK: Oxford University Press.
- Smith, B. D., Tun, M. T., Chit, A. M., Win, H., & Moe, T. (2009). Catch composition and conservation management of a human–dolphin cooperative cast-net fishery in the Ayeyarwady River, Myanmar. *Biological Conservation*, *142*, 1042–1049.
- Smith, T., & Siniff, D. (1981). Coordinated behavior of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology*, *59*, 1185–1189.
- Smolker, R. A. (2001). *To touch a wild dolphin*. New York, NY: Anchor Books.
- Smolker, R. A., & Pepper, J. (1999). Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology*, *105*, 595–617.
- Smolker, R. A., Mann, J., & Smuts, B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology*, *33*, 393–402.
- Smolker, R. A., Richards, A. F., Connor, R. C., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): A foraging specialization involving tool use? *Ethology*, *103*, 454–465.
- Sol, D. (2003). Behavioural flexibility: A neglected issue in the ecological and evolutionary literature. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 63–82). Oxford, UK: Oxford University Press.
- Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist*, *172*, S63–S71.
- Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology*, *2*, 77–89.
- Tavolga, M. C. (1966). Behavior of the bottlenose dolphin (*Tursiops truncatus*): Social interactions in a captive colony. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 718–730). Oakland, CA: University of California Press.
- Taylor, C., & Saayman, G. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, *44*, 286–298.
- Terry, R. (1986). The behaviour and trainability of *Sotalia fluviatilis guianensis* in captivity: A survey. *Aquatic Mammals*, *12.3*, 71–79.
- Thomas, B. (1970). Notes on the behavior of the killer whale *Orcinus orca* (Linnaeus). *The Murrelet*, *51*, 10–11.
- Torres, L. G., & Read, A. J. (2009). Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Marine Mammal Science*, *25*, 797–815.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1971* (pp. 136–179). Chicago, IL: Aldine.
- Tyack, P. L. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, *8*, 105–116.
- Tyack, P. L. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, *18*, 251–257.
- Tyack, P. L. (2000). Functional aspects of cetacean communication. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean Societies, field studies of dolphins and whales* (pp. 270–307). Chicago, IL: The University of Chicago Press.

- Van Parijs, S. M., & Corkeron, P. J. (2001). Evidence for signature whistle production by a Pacific humpback dolphin, *Sousa chinensis*. *Marine Mammal Science*, 17, 944–949.
- Visser, I. N. (1999). Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science*, 1, 220–227.
- Visser, I. N. (2000). Killer whale (*Orcinus orca*) interactions with longline fisheries in New Zealand waters. *Aquatic Mammals*, 241–252.
- Visser, I. N., Smith, T. G., Bullock, I. D., Green, G. D., Carlsson, O. G. L., & Imberti, S. (2008). Antarctic peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science*, 24, 225–234.
- Ware, C. R., Wiley, D. N., Friedlaender, A. S., Weinrich, M. T., Hazen, E. L., Bocconcelli, A., et al. (2014). Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A.. *Marine Mammal Science*, 30, 494–511.
- Watson-Capps, J.J. (2005). Female mating behavior in the context of sexual coercion and female ranging behavior of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia (PhD thesis) (p. 195). Washington, DC, Georgetown: Department of Biology, Georgetown University.
- Watwood, S. L., Tyack, P. L., & Wells, R. S. (2004). Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, 55, 531–543.
- Weilgart, L. S., & Whitehead, H. (1993). Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. *Canadian Journal of Zoology*, 71, 744–752.
- Weinrich, M. T. (1991). Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Canadian Journal of Zoology*, 69, 3012–3019.
- Weinrich, M. T., Rosenbaum, H., Scott Baker, C., Blackmer, A. L., & Whitehead, H. (2006). The influence of maternal lineages on social affiliations among humpback whales (*Megaptera novaeangliae*) on their feeding grounds in the southern gulf of Maine. *The Journal of Heredity*, 97, 226–234.
- Weinrich, M. T., Schilling, M., & Belt, C. (1992). Evidence for acquisition of a novel feeding behaviour: Lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour*, 44, 1059–1072.
- Whitehead, H. (2003). *Sperm whales: Social evolution in the Ocean*. Chicago, IL: University of Chicago Press.
- Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies, field studies of dolphins and whales* (pp. 219–246). Chicago, IL: The University of Chicago Press.
- Whitehead, H., Rendell, L. E., Osborne, R. W., & Würsig, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: Review and new directions. *Biological Conservation*, 120, 427–437.
- Wiley, D., Ware, C. R., & Bocconcelli, A. (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, 148, 575–602.
- Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). Killer appetites: Assessing the role of predators in ecological communities. *Ecology*, 85, 3373–3384.
- Würsig, B. (2008). Playful behavior. In W. F. Perrin, B. Würsig, & J. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 885–888). Burlington, MA: Academic Press.
- Würsig, B., & Dorsey, E. (1989). Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, wumming in the Beaufort Sea. *Aquatic Mammals*, 15.1, 27–37.
- Wyles, J. S., Kunkel, J. G., & Wilson, A. C. (1983). Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 80, 4394–4397.
- Wyman, J. (1863). Description of a “white fish,” or “white whale,” (*Beluga Borealis*, Lesson). *Boston Journal of Natural History*, 7, 603–612.
- Yamagiwa, J., & Karczmarski, L. (2014). *Primates and cetaceans: Field research and conservation of complex mammalian societies*. New York, NY: Springer.

- Yano, K., & Dahlheim, M. E. (1995). Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. *Fishery Bulletin*, 93, 355–372.
- Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., & Matkin, C. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63, 1103–1119.

Commentary on Chapter 4: Proto-c Creativity?

Learning from nature is almost absent from discussions of creativity in psychology. Building on the more or less implicit assumption that creativity is an eminently human capacity, researchers focus first and foremost on understanding the high-end cultural manifestations of creativity as embodied in the work of geniuses. It is in the last decades that everyday life creative acts came to be studied intensely (see Glăveanu, 2011; Richards, 2007). However, the boundaries of creativity are still strictly guarded by constant references to intentionality, consciousness, knowledge, etc., to the marginalization and almost exclusion of children, the “mentally ill,” and nonhuman animals. When they are inspired by nature, creativity researchers tend to keep this inspiration at the level of metaphor or analogy (see for example Simonton’s (1999) account of how ideas are generated and selected through what resemble Darwinian processes). Real efforts to bridge human and nonhuman creativity are still rare (for an exception, see Kaufman & Kaufman, 2014) and yet we can’t help but feel intrigued by behaviors like the milk smoking in the case of Dolly, a bottlenose dolphin calf, the starting point for Patterson and Mann’s (this volume) discussion of cetacean innovation. “Is this really creativity?” one might ask, persuaded by the current status quo. If nothing else, it is a behavior that generates surprise and, at least for Bruner (1962), this is a key creativity marker.

The central question a creativity scholar has when approaching a chapter like the one referred to above is: what exactly is the “core” of creativity in cetaceans and, by extension, in nonhuman animals? The two authors offer us valuable insights into this by referring to behavioral plasticity, to the capacity of dolphins and whales to act flexibly in an ever-changing environment and to respond in novel ways to both new and old stimuli. The essence of creativity in human and nonhuman animals alike relates in the end to *difference*, acting in an open and nonpre-determined manner in ways that generate novelty. When our behavior is not the direct consequence of environmental conditions, not a

reflex reaction but a new response to what the environment has to offer, then I believe we are facing the roots of all creative expression. In order to act differently (and, thus, creatively to some extent), organisms need to find mechanisms to distance themselves from the here and now of perception and of their immediate situation. Such distancing is ensured in the case of humans by the development of the symbolic function (Vygotsky, 1997). Not many nonhuman animals are credited with the capacity to form and use signs however so, consequently, they are denied “human” (symbolic) creativity. But the theoretical question remains of whether action can or should be catalogued simply as either symbolic or non/pre-symbolic. In their chapter, Patterson and Mann offer us a wealth of illustrations of flexible and atypical behavior in wild and captive whales and dolphins that come to challenge strict divisions between the two.

The starting point in their analysis of cetacean innovation can be found in the relation between organism and its environment. The two authors list preconditions for creativity that include the close relation between features of the organism (like behavioral plasticity, ability to learn, neophilic tendencies), and properties of its context and surroundings (e.g., the existence of free time and extended maternal care, social or group living, and reduced predation risk). In an effort to summarize what seem to be a set of “minimal” conditions for creativity to develop, we are being introduced in the chapter to a detailed discussion of how variations in these conditions can lead to differences in creative expression, in both its content and level, within and most of all between species. At the end it is hard to say for the two authors if a stable environment with abundant resources will always increase the chances of innovation or if, on the contrary, challenging circumstances (marked by tourism, fishing, food shortages, etc.) are not actually more beneficial as they constrain the animal to create or perish. The idea of “optimal conditions” for creativity, where challenges stimulate but don’t block new behaviors, would perhaps be useful here.

The complexity of cetacean innovation is reflected in their often intricate cooperative behavior and interaction with objects. Just as in the case of human creativity (see Glăveanu, 2011, 2014), social relations are crucial in making behaviors flexible and thus potentially creative. Interacting with members of one’s own species not only “socializes” the individual but also offers examples of plastic and adaptive actions that can be, in turn, copied and modified. Moreover, contact with members of other, distant groups or individuals can increase one’s repertoire of actions; e.g., in the case of whales, the transmission and variations of “songs” during the breeding season. This is reminiscent of Bartlett’s (1923) old assumption that creativity emerges when members of two different communities or cultures come into contact. Perhaps more

intriguingly, Patterson and Mann also give examples of cooperation with members of other species, including fishermen, and even episodes of cetaceans trying to reciprocate in the relationship. On the other hand, we have numerous illustrations of whales and especially dolphins creating and using tools. In ways that were reminiscent of functional creativity (Cropley & Cropley, 2010), dolphins in captivity were noticed scraping the tank floor with tools used by divers (and later, when these were removed, with pieces of broken tile) and eating the sea lettuce that came loose or, in the wild, detaching sponges from the seafloor to use them later as protection when probing rocks or shells in search of prey. If the examples above foreground the utility of such potentially creative acts, it is play activities, primarily among calves, that offer an even wider range of opportunities for creativity serving no apparent practical reason (but only apparently, see Kuczaj & Eskelinen, 2014a, 2014b). Patterson and Mann describe the playful interaction of two bottlenose dolphin calves at Marineland in Florida, in which they engaged in a game of fetch. Most interestingly, the two partners often switched roles and repeated the whole process in ways that remind of position-exchange exercises, a precondition for the development of agency and symbolic representation (Gillespie, 2012). In fact, the roots of an early capacity to take the perspective of another in the situation is demonstrated also by the surprising finding that dolphins can produce novelty on demand (when instructed to “create”), both individually and in tandem. I would argue that this is not only a matter of remembering what was done in that session (Kuczaj & Eskelinen, 2014a, 2014b), but a sign of grasping what is intended and perceived by the trainer.

The capacity to recognize novelty is considered by Kaufman and Kaufman (2004) as the first level of animal creativity. The two authors devised an interesting creativity framework for animal cognition that includes, alongside the recognition of novelty, observational learning and innovative behavior. Although one might be tempted to see this as a hierarchy, the authors made clear the fact that each creativity marker should be studied in its own right and that animals, for instance, don't necessarily have to master observational learning before showing signs of innovative behavior (which in this case is represented by the ability to create a tool or behavior that is new and different and perceive it as such). In order to avoid hierarchical readings of their model, the framework was elaborated further as a creativity spectrum (see Kaufman, Butt, Kaufman, & Colbert-White, 2011). This conception resembles to some extent an understanding of creative action as discussed previously, including habitual, improvisational, and innovative creativity (Glăveanu, 2012). In both cases, innovative behavior is considered the one that results in more or less “deliberate” novelty (although the intentionality of this process in the case of animals can be debated).

Patterson and Mann actually chose to focus in their chapter on cetacean innovations because they consider them to be the implementation of novelty in a useful way. In contrast, creativity for the two authors relates more to the underlying cognitive processes that generate novelty. The difficulty of capturing such processes in the case of nonhuman animals in fact led many animal cognition scholars to study innovative outcomes (see also Boogert, Reader, Hoppitt, & Laland, 2008) and consider innovations at an individual level instead of entire populations (Ramsey, Bastian, & van Schaik, 2007). This separation between mental processes and behavior, reflected also in the broader distinction made today between idea generation (creativity) and idea implementation (innovation), is problematic as it portrays creativity as a purely cognitive affair (for a critique, see Glăveanu, 2014). Such a reductionist reading is not productive for either human or animal creativity; in the case of the former it ignores the materiality of creative action, in that of the latter it makes creativity virtually impossible to study as such without direct access to cognition.

Instead of using this problematic criterion I consider it more useful to think about what type of creativity we are talking about in the case of cetaceans and nonhuman animals more widely. A comprehensive typology for human creativity, taking into account person, product, and process, has been proposed by Kaufman and Beghetto (2009) and it differentiates between mini-, little-, Pro-, and Big-c creative acts. Kaufman and Kaufman (2014) applied this four C model to animal studies and concluded that mini-c is characterized in this case by the situation-specific innovations of a single individual, little-c emerges when a second animal joins the first in performing the novel behavior, and Pro-c is reserved for expert innovators (like Imo, the Japanese macaque who discovered potato and wheat washing). Of course, Big-c creativity, which in humans relates to achievements celebrated by an entire society and therefore requires the existence of accumulated culture, translates poorly to the animal kingdom. While the aim of making distinctions between forms or levels of animal creativity is certainly worthwhile, a discussion of the four C model in this area remains at the level of analogy. Between the mini-, little-, or Pro-c creativity of humans and that of nonhuman animals there is not only a difference of degree but, in most cases, a qualitative leap enforced by the fact that humans structure their (creative) action symbolically (Glăveanu, 2014; Vygotsky, 1997). This reflection, as well as the rich illustrations of whale and dolphin innovations offered by Patterson and Mann, make me consider whether it wouldn't be more appropriate to actually expand the four C model to a five C one and include what I would call, in lack of a better term, *proto-c creativity*. This for me is the creativity intrinsic to organisms exist as dynamic, open systems, acting within environments marked by

variability and change. Behavioral flexibility and adaptability are the essence of proto-c creativity and they constitute the basis for other, more elaborate creations or innovations in both humans and animals. Proto-c is the creativity of action that precedes and accompanies symbolic forms of creativity such as little-c, built on reinterpretations of experience. Postulating the existence of proto-c therefore solves a complicated theoretical dilemma: is there creativity outside and beyond symbolically mediated activity, before the use of language? The playful activities of cetacean calves, just like those of a human infant, compel us not only to at least consider this conceptual possibility, but also engage in a much closer study of habits, acts of imitation and copying (see also Glăveanu, 2012). Patterson and Mann report, for the latter, cases of dolphins imitating the behavior of turtles, penguins, and even humans, and of whales copying the whistle sounds of close associates in the process of developing their signature vocalizations.

In the end, proto-c is not outside or before “real” creativity but it is the basis for the creative action of humans and animals alike. It is also not separate from the creativity involved in mini-, little-, Pro-, and Big-c creative acts. In the case of cetaceans in fact, most of the examples offered by Patterson and Mann illustrate simultaneously proto- and mini-c forms of creativity in which cetaceans experiment with new forms of action and interaction and become then capable of reproducing and varying them, arguably while recognizing their novelty. The domain generality of creativity claimed by the two authors is in fact the generality of a proto-c form of creative expression. As we move toward the more elaborate little-, Pro-, and especially Big-c types there is much more room for variation depending on the characteristics of the individual, the domain, and the field or audience. Kaufman and Kaufman (2004, p. 144) were right to say that conceptualizing creativity in animals can not only shed light on animal cognition but also expands our current understanding of creativity. Big-c creative achievements in human societies might stand out like mountaintops in our current perception, but we should not forget they emerge out of a sea of proto- and mini-c expressions and are constantly nurtured by these. Looking toward and inside this sea (pun intended) is greatly facilitated by ongoing research on cetacean innovation aptly summarized in this book.

References

- Bartlett, F. C. (1923). *Psychology and primitive culture*. Cambridge: Cambridge University Press.
- Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, 75, 1509–1518.
- Bruner, J. (1962). *On knowing: Essays for the left hand*. Cambridge: Belknap Press.

- Cropley, D., & Cropley, A. (2010). Functional creativity: "Products" and the generation of effective novelty. In J. C. Kaufman, & R. J. Sternberg (Eds.), *The Cambridge handbook of creativity* (pp. 301–317). Cambridge: Cambridge University Press.
- Gillespie, A. (2012). Position exchange: The social development of agency. *New Ideas in Psychology, 30*(1), 32–46.
- Glăveanu, V. P. (2011). Creativity as cultural participation. *Journal for the Theory of Social Behaviour, 41*(1), 48–67.
- Glăveanu, V. P. (2012). Habitual creativity: Revising habit, reconceptualizing creativity. *Review of General Psychology, 16*(1), 78–92.
- Glăveanu, V. P. (2014). *Distributed creativity: Thinking outside the box of the creative individual*. Cham: Springer.
- Kaufman, A. B., & Kaufman, J. C. (2014). Applying theoretical models on human creativity to animal studies. *Animal Behavior and Cognition, 1*(1), 77–89.
- Kaufman, A. B., Butt, A. E., Kaufman, J. C., & Colbert-White, E. N. (2011). Towards a neurobiology of creativity in nonhuman animals. *Journal of Comparative Psychology, 125*(3), 255–272.
- Kaufman, J. C., & Beghetto, R. A. (2009). Beyond big and little: The four C model of creativity. *Review of General Psychology, 13*(1), 1–12.
- Kaufman, J. C., & Kaufman, A. B. (2004). Applying a creativity framework to animal cognition. *New Ideas in Psychology, 22*, 143–155.
- Kuczaj, S. A., & Eskelinen, H. C. (2014a). Why do dolphins play? *Animal Behavior and Cognition, 1*(2), 113–127.
- Kuczaj, S. A., & Eskelinen, H. C. (2014b). The "creative dolphin" revisited: What do dolphins do when asked to vary their behavior? *Animal Behavior and Cognition, 1*(1), 66–77.
- Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences, 30*, 393–437.
- Richards, R. (2007). *Everyday creativity and new views of human nature: Psychological, social, and spiritual perspectives*. Washington, DC: American Psychological Association.
- Simonton, D. K. (1999). *Origins of genius: Darwinian perspectives on creativity*. New York, NY: Oxford University Press.
- Taylor, C., & Saayman, G. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour, 44*, 286–298.
- Vygotsky, L. S. (1997). The history of the development of higher mental functions. In R. W. Rieber (Ed.), *The collected works of L.S. Vygotsky* (Vol. IV, pp. 1–251). New York, NY: Plenum Press.