



Is Enrichment Always Enriching and How Would You Know? Unintended Consequences and the Importance of Formal Assessment of Enrichment Programs in Bottlenose Dolphins (*Tursiops truncatus*)

Heidi Lyn^{1,2}, Hannah Bahe^{2,3}, Megan S. Broadway^{2,4}, Mystera M. Samuelson^{2,5}, Jamie K. Shelley², Tim Hoffland², Emma Jarvis², Kelly Pulis², Delphine Shannon², and Mobashir Solangi²

¹University of South Alabama, USA

²Institute for Marine Mammal Studies, USA

³The University of Southern Mississippi, USA

⁴University of Louisiana at Monroe

⁵The University of Nebraska Medical Center

Bottlenose dolphins (*Tursiops truncatus*) are viewed as a highly intelligent species capable of complex behaviors. This requires marine parks to maintain dynamic environmental enrichment programs in order to ensure dolphins' optimal psychological and physiological well-being while in human care. In this study, two experiments were conducted to determine the effects of different forms of enrichment on the behavior of four bottlenose dolphins. In Experiment 1, multiple forms of novel enrichment resulted in a shift away from individual swim patterns – a change that is associated with increased behavioral diversity and so often considered an improvement in animal welfare – but also resulted in avoidance behavior and initially resulted in a decrease in affiliative behavior. In Experiment 2, introducing choice of enrichments resulted in unintended social consequences, such as agonistic behaviors. These two experiments together demonstrated that interpreting the results of enrichment programs may not be as straightforward as often presumed. The results suggest that unique forms of enrichment and variable schedules might be particularly effective but also that consistent evaluation continues to be necessary to minimize unintended behavioral consequences.

Keywords: animal welfare, bottlenose dolphins, environmental enrichment, *Tursiops truncatus*

In recent decades, increased emphasis has been placed on understanding and developing new and innovative methods of fostering optimal welfare conditions for animals under human care (Broom, 2011). This is particularly true for charismatic megafauna, such as big cats, elephants, nonhuman primates, and marine mammals (Hosey et al., 2020). Even more specifically, environmental enrichment programs are the principle technique used to improve animal welfare through the addition of stimuli to animal enclosures. The term *enrichment* can be defined in multiple ways, one notable difference being the requirement that the enrichment actually improves the welfare of the animal (Clegg & Delfour, 2018; de Azevedo et al., 2007). For the purposes of this paper, we define *environmental enrichment* as any alterations made to an animal's environment for the purposes of improving its biological or cognitive welfare (see Bloomsmith et al., 1991; Hoy et al., 2010; Swaisgood & Shepherdson, 2005, for similar usage of the term enrichment). Attempts to define enrichment based on the resulting improvement in welfare, or lack thereof, are problematic because 1) it would only be appropriate to refer to a modification program as enrichment after it has been shown to be successful at some arbitrary endpoint, 2) measures of success in improving welfare have not been thoroughly assessed, well defined, or universally agreed upon, and 3) formal assessments of the success of an enrichment program are rarely conducted, so the results of the enrichment program would never be known. If successful, environmental enrichment programs result in the reduction of repetitive stereotypic behaviors and/or an increase in

Please send correspondence to Heidi Lyn, hlyn@southalabama.edu <https://doi.org/10.46867/ijcp.2020.33.04.01>

* Special Issue: Revisiting The Legacy of Stan Kuczaj

exploratory behaviors and species typical behaviors (Carlstead, 1998; Mellen & MacPhee, 2001; Shepherdson, 1998; Wells, 2009). Providing environmental enrichment has become standard practice and is now a requirement for facilities that are accredited by the Association of Zoos and Aquariums (AZA), which also provides recommendations and protocols for specific species and taxa housed in AZA-accredited facilities (Association of Zoos and Aquariums, 2020).

Although the pursuit of optimal welfare strategies and widespread use of environmental enrichment for animals in human care is commendable, it is important to also note that these procedures are rarely formally assessed within zoological institutions using scientific methodology. Instead, nonsystematic methods and subjective measures are typical, if an assessment is conducted at all. This approach leaves some question as to the effectiveness of various enrichment programs (Broom, 1988; Canali & Keeling, 2009; Clegg & Delfour, 2018; Delfour & Beyer, 2012; Hoy et al., 2010; Makecha & Highfill, 2018; Newberry, 1995), which range from simply adding objects to an enclosure to social housing (Daoudi et al., 2017; Yeater et al., 2013), training (Ramirez, 1999; Westlund, 2014), introducing scent (Nelson Slater & Hauber, 2017; Samuelson et al., 2016), or supplying more naturalistic or challenging feeding opportunities (Fernandez & Timberlake, 2019; McPhee, 2002; Wagman et al., 2018) to name a few. There is evidence that some enrichment programs may even result in an increase in unwanted behaviors, such as increased aggression (Franks et al., 2009), manipulation of the enrichment to the point in which it becomes dangerous for the animals (Hahn et al., 2000; Hare et al., 2007), or other undesirable behaviors (Bloomsmith et al., 1991). Systematically monitoring the animals' responses to environmental enrichment can allow researchers to evaluate, in a nonbiased fashion, enrichment programs' welfare outcomes (Delfour & Beyer, 2012; Samuelson et al., 2016; Shyne, 2006).

When evaluating an enrichment program, the enrichment is generally thought to be successful if physiological health improves and if an increase in species-typical behaviors and a decline in repetitive stereotypical behaviors are observed after its introduction (Mason, 1991; Shyne, 2006). Stereotypies are typically defined as repetitive, unvarying behaviors that have no obvious function or goal (Mason, 1991). Stereotypies are also usually more difficult to disrupt than typical behaviors and have often been assumed to be associated with poor animal welfare by scientists and the public alike (Mason et al., 2007; Miller, 2012; Miller, Mellen, et al., 2011). However, more and more frequently, the assumption of this link between presumed stereotypies and poor welfare has been questioned (Clegg et al., 2017; Franks et al., 2009; Greening, 2019; Miller, Kuczaj, et al., 2011; Poirier & Bateson, 2017).

Enrichment programs and their welfare outcomes for bottlenose dolphins have received a lot of attention in recent years; however, formal assessments of said programs are still needed (Clark et al., 2013; Clegg et al., 2017; Clegg & Delfour, 2018; Makecha & Highfill, 2018). In bottlenose dolphins under human care, the most prominent species-typical behaviors examined are affiliative social behaviors (Waples & Gales, 2002), exploratory and play behaviors (Kuczaj et al., 2002), swimming patterns (Gygax, 1993) and vocalizations known to be associated with these behavior states (Jones et al., 2020).

Alternately, the most frequently observed stereotypical behavior in bottlenose dolphins in managed care is repetitive circle swimming (Brando et al., 2018; Clark, 2013). There is considerable debate regarding whether certain repetitive behaviors, such as circle swimming, actually represent a threat to welfare (Brando et al., 2018; Clark, 2013; Clegg et al., 2017; Clegg & Delfour, 2018; Makecha & Highfill, 2018; Miller, Kuczaj, et al., 2011; Miller, Mellen, et al., 2011; Serres et al., 2020). However, because this behavior often correlates with a decreased overall behavioral diversity, it has been historically considered to be an undesirable behavior, described as stereotypical due to its repetitive nature (Fernandez & Timberlake, 2019; Franks et al., 2009; Miller, Mellen, et al., 2011; Pomerantz et al., 2013). Thus, circle swimming is commonly regarded as a cause for concern and is included in evaluations of enrichment and animal welfare (Brando et al., 2018; Clegg et al., 2015; Miller, Mellen, et al., 2011; Ugaz et al., 2013). The reasons for which dolphins may engage in a stereotypical swim pattern are generally unknown, but possible causes include lack of stimulation, frustration, and the kinesthetic needs of animals with large territories (Eilam et al., 2006; Franks et al., 2009; Mason et al., 2007; Miller, Kuczaj, et al., 2011). Because the term *stereotypical* has a long history of being misrepresented in the literature and colloquially within zoological facilities, we will preferentially use the term individual

swim pattern (ISP), as has been done in previous studies (e.g., Franks et al., 2009).

Unfortunately, few studies present research focused on the possible unintended consequences of environmental enrichment or on individual differences in animals' reactions to enrichment programs (Bayne, 2005; Carlstead, 1991; Hare et al., 2007; Hoy et al., 2010). In many dolphin facilities, enrichment programs are primarily focused on toy making (Brando et al., 2018; Clark, 2013; Delfour & Beyer, 2012; Kuczaj et al., 2002), with little scientific monitoring of behavioral interest or engagement with the toys. When there is behavioral monitoring, the effects of enrichment items are sometimes unclear and context-dependent (Delfour & Beyer, 2012; Neto et al., 2016). In some cases, the addition of enrichment even shifts social engagement to more undesirable behaviors, for example, gate-guarding in a beluga whale after the introduction of a novel enrichment item (Lyn, 2009).

The focus on objects/toys as enrichment can also be problematic. Dolphins are known to exhibit changes in both the frequency and type of play behaviors exhibited throughout the lifespan (Highfill & Kuczaj, 2007). As with many species, young dolphins are more likely than adults to engage in object play (Bekoff & Byers, 1992; Delfour et al., 2017; Eskelinen et al., 2015; Pace, 2000); however, responses to objects vary on an individual basis (Neto et al., 2016), and even young animals may not interact with objects placed in the enclosure (Delfour & Beyer, 2012). Also, because dolphins are living longer under human care (Jaakkola & Willis, 2019), like most long-lived species, dolphins require an adjustment to enrichment throughout the lifespan (Franks et al., 2009; Kuczaj et al., 2002; Lyn, 2009; Rumbaugh et al., 1989). Therefore, although important (Delfour et al., 2017; Makecha & Highfill, 2018), the mere presence of objects intended as environmental enrichment devices cannot be assumed to constitute enrichment.

To examine what types of enrichment may be the most successful for dolphins in human care, we consider variations to both object type and object presentation. Challenges, such as the introduction of highly novel objects, produce temporary periods of stimulation that broaden the experience of the individual allowing them to better predict and adapt to future events (Blum, 2002; Weiss, 1971). Similarly, several studies have suggested that control over one's environment leads animals to become more adaptable (Mellen & MacPhee, 2001). For example, rats that were given control over an aspect of their environment (i.e., turning a light on or off) showed increased cognitive abilities when compared to rats without environmental control (Alliger & Moller, 2011). It is possible that a combination of control over the environment and exposure to environmental challenges may be successful for the enrichment of wildlife in human care, particularly those prone to stereotypic behavior when there is a lack of cognitive complexity in their environment (see Clark, 2013).

The present study sought to examine the effects of various forms of objects (established enrichment devices, modified enrichment devices, and highly novel objects) (Experiment 1) and choice (Experiment 2) on the behavior of four bottlenose dolphins in human care. While the sample size is limited, we believe these preliminary results are illustrative of the potential unexpected consequences of enrichment programs.

In Experiment 1, the behavior of two mature bottlenose dolphins (one male and one female) were observed before, during, and after the introduction of three different forms of enrichment (Table 1). Behavioral diversity, changes in frequency and duration of stereotypical behaviors (including regurgitation), and species-typical behaviors were recorded. Experiment 2 examined the role of choice as an enrichment tool by allowing a young male dolphin to choose between two of these possible enrichment items. Behavior was observed before, during, and after the choice was presented in order to assess potential behavioral changes exhibited by the four individual dolphins in the environment.

Table 1

Description of Enrichment and Baseline Conditions with Examples of Items Used During Each Condition

Condition	Treatment
Baseline 1	Standard enrichment toys (e.g., balls, hoops, buoys)
Enrichment 1	Standard enrichment toys plus novel floating objects with tactile features (e.g., large barrels covered in artificial turf material 10' of braided rubbing rope attached to floats)
Baseline 2	Standard enrichment toys
Enrichment 2	Standard enrichment toys plus social enrichment – researchers and volunteers attempting to gain the attention of the dolphins by interacting with standard and novel toys (e.g., people interacting with water sprayers, hoses, remote controlled toys, a small raft, and standard toys)
Baseline 3	Standard enrichment toys
Enrichment 3	Standard enrichment toys plus large highly novel, semiactive items (e.g., bubble apparatus, large kelp toys, large blocks of ice)
Baseline 4	Standard enrichment toys

Experiment 1

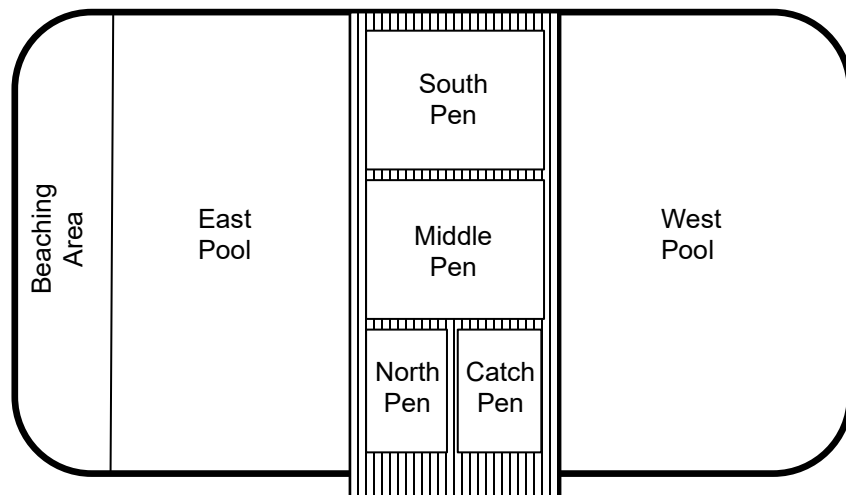
Method

Subjects

In the first experiment, two mature (>30 years old) bottlenose dolphins (*Tursiops truncatus*) served as participants. Bo (female) and Buster (male) were housed in a pool complex (Figure 1) at the Institute for Marine Mammal Studies (IMMS) in Gulfport, Mississippi, USA.

Figure 1

Pool Layout



Outside of regular training sessions, the animals had access to a random assortment of approximately five to eight environmental objects, pulled from a constantly changing pool of over 30 items created by the animal care staff as enrichment devices.

These items included various floats, balls, and hoops (examples in Table 1). Regular enrichment items were removed during training sessions and returned to the pool afterwards.

Experimental Design

Novel objects were introduced in an A-B-A-C-A-D-A design where A was a baseline condition that included the dolphins' standard enrichment items – the other conditions were Enrichment Conditions 1-3 (see Table 1). Each condition lasted one week (7 days).

Enrichment 1 included baseline objects as well as newly constructed objects that were similar to the baseline objects but that included novel tactile materials. For example, barrels covered in artificial turf material and a rubbing rope. This condition was designed to test standard variations on toys that were added to the environment in a typical fashion (added and only removed for brief periods while training was in session).

Enrichment 2 explored the effects of increased social interaction with people during five 15-min interaction sessions each day. These social interaction sessions included researchers and volunteers who could choose to utilize toys that included the regular enrichment devices, or water guns, a large ball, a water hose and sprayer, or a remote-control boat. These objects were manipulated by humans and used in numerous ways to stimulate the dolphin's curiosity and gain their attention. If dolphins appeared to actively avoid or become agitated by a particular toy or interaction, then that type of interaction was discontinued, and other toys/interactions were used for the remainder of the session. Agitated behavior was defined as displacement, avoidance, aggressive, or anxious behaviors (e.g., jaw popping, tail slapping, chuffing, charging, or repeatedly breaching; Table 2). Enrichment 2 was designed to test the effects of added opportunity for social interaction, in which the dolphins could choose to participate if they so desired.

Enrichment 3 included larger items that were considered more stimulating than typical toys. These included underwater objects such as a large block of ice (a 2 ft diameter, 3 ft high garbage can, filled and frozen), a bubble stream generating apparatus, and sinking kelp made from 4 in. wide, 3 ft long strips of car wash material (thick, felt-like fabric). Only one of these objects was introduced each day, and each was removed from the pool after 2 hr, except the ice which was allowed to melt in the pool – a process that took up to 8 hr.

Data Collection

Data were collected by IMMS research staff members who recorded behavioral data using an iPad and Numbers software application. Data were recorded during fifteen 1-min intervals twice daily (once on weekend days). Observation times were pseudo-randomly chosen from six potential time slots chosen to be at least 30 min from scheduled feeding times. Observers were trained during a minimum of three practice observation sessions, and reliability was assessed during group observation sessions. The behavioral data categories reported all reached a minimum of 85% reliability among observers.

Recorded behaviors are defined in Table 2. Swim behaviors and location were determined by scan sampling at the top of every minute. All other behaviors were coded as either present or absent during each interval. Circle swimming was defined as a minimum of three revolutions of the larger pool (Miller, Mellen, et al., 2011). However, in practice, both dolphins had an easily identified ISP, which was readily detected within the first revolution (e.g., Bo would swim counterclockwise $\frac{3}{4}$ of the perimeter, then cut across the northwest corner).

Data Analysis

All data were collapsed across individual sessions for analysis, resulting in a session score for the numbers of intervals (out of 15) in which each behavior occurred. One-way ANOVAs allowed for enrichment versus baseline conditions as well as individual condition-by-condition comparisons for each dolphin and each behavior across the seven conditions. ANOVAs were followed by post hoc Fisher LSD tests to pinpoint any significant differences between conditions.

Table 2

Operational Definitions for Swim Behaviors, Habitat Location, and Secondary Behaviors (All Behaviors were Considered Exclusive)

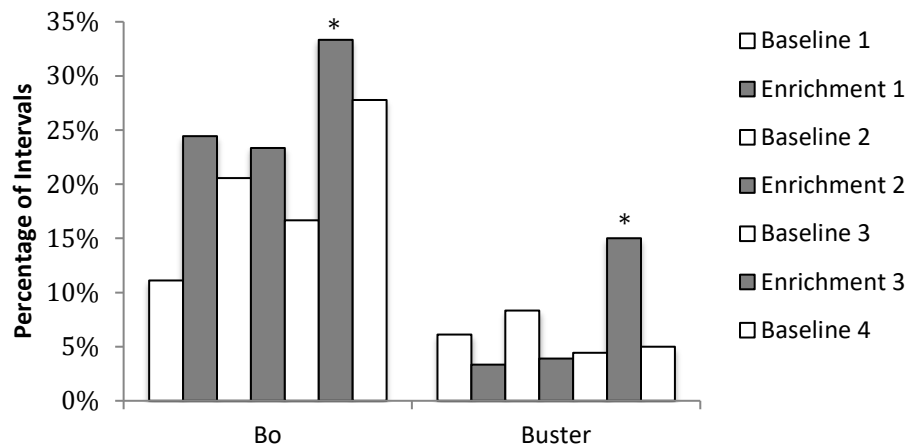
Swim Behaviors	Definition
Circle swim	A dolphin swimming in a repetitive pattern around the perimeter of the pool – minimum 3 revolutions; stereotypic behavior/individual swim pattern (ISP); see text for more details
Non-circle swim	A dolphin swimming in irregular patterns around the pool
Pair swim	Both dolphins swim together and surface in synchrony; dolphins must surface together in synchrony at least once while swimming together in order to be classified as a pair swim
Stationary	Dolphin is floating in one location or still at the bottom of the tank; swim behaviors were exclusive and were not dually coded
Location	Definition
East pool deep	East side of the pool, 16 m × 19.8 m × 3.6 m
Beaching area	Shallow area of the East pool, 0.91 m deep
West pool	West side of the pool, 16 m × 19.8 m × 3.6 m
South pen	Located between the East and West pools, 6 m × 6 m
Middle pen	Located between the East and West pools, 6 m × 6 m
North Pen	Located between the East and West pools closest to the East pool, 3 m × 6 m
Catch pen	Located between the East and West pools closest to the West pool, 3 m × 6 m
Secondary Behaviors	Definition
Affiliative behavior (Experiment 1)	One dolphin is in physical contact with the other with no evidence of aggression (no biting, raking, or charging); this also includes any instance in which a dolphin focuses its attention towards another dolphin or person including looking at, touching, or acting in response to another individual
Affiliative activity (Experiment 2)	Included the above behaviors but was expanded to include include group swimming, orienting toward another dolphin, touching another dolphin, chase/following, flee/avoidance, tooth raking, and chin or tail slapping
Interference (Experiment 2)	One dolphin moving between another dolphin and the toy with which they were interacting
Object play	A dolphin is in physical contact with an object for more than 1 s; this includes throwing objects into the air, pulling object underwater, pushing object with rostrum, etc.; also includes maintaining constant contact with objects; based on standard definitions of play (intrinsically rewarding behavior not linked to immediate survival; e.g., Janik, 2015)
Regurgitation	Expelling previously ingested food; regurgitation was included as a behavior of concern as it had been previously observed as a stereotypy in Buster; however, it did not occur frequently enough during the studies for analysis
Aggression/ displacement	One dolphin bites, rakes, or charges another; one dolphin attempts to enter a pool area and is blocked by the other

Results

Bo showed increased non-circle swims during enrichment sessions versus non-enrichment sessions, $F(1, 82) = 3.93, p = .05$, but Buster did not, $F(1, 82) = 0.43, p = .51$. However, when analyzing each session individually, Buster did show a significant increase in non-circle swims during Enrichment 3, when the extremely novel forms of enrichment were present, $F(6, 77) = 2.23, p < .05$. Post hoc tests showed that this non-circle swimming increase for Buster in Enrichment 3 applied to all other conditions (Mean Difference ranged from 1.33-1.75, all $p = .025$) apart from Baseline 2, which was approaching significance (MD = 1.00, $p = .088$) (see Figure 2). In contrast, Bo's non-circle swims did not significantly differ across the enrichment conditions as a group, $F(6, 77) = 1.95, p = .08$, but, due to the findings with Buster, an LSD post hoc test was run and showed a significant increase in non-circle swimming in Enrichment 3 (the condition with the most novel items) compared to Baseline 1 (MD = -3.33, $p < .003$) and Baseline 3 (MD = 2.50, $p = .026$).

Figure 2

Percentage of Intervals that were Coded as Non-circle Swims over the Baseline and Enrichment Conditions for Each Dolphin



Note. * indicates that non-circle swims were significantly more frequent in Enrichment 3 than the other condition.

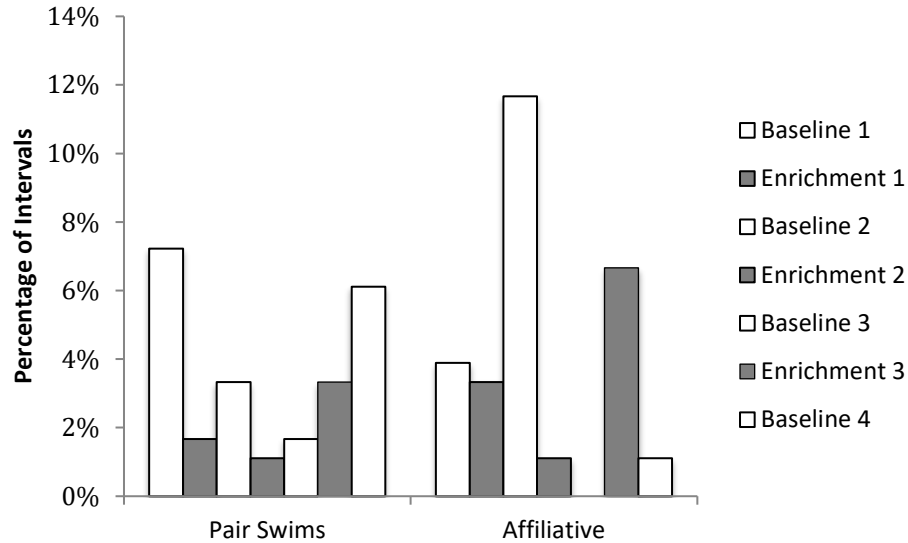
The dolphins also altered their usage patterns of the East pool during Enrichment 3, likely avoiding the area because the highly novel enrichment was deployed there. Bo averaged 70% of her intervals in the East pool across the baseline conditions, and Buster averaged 76%. The East pool was also where the majority of their behaviors of concern were reported (including abnormal time spent interacting with a specific toy, and consistent food regurgitation). In Enrichment 3, in contrast, Bo spent only 49% of her intervals in the East Pool and Buster 61%.

None of the other behaviors showed significant effects across all enrichment conditions. However, it is of interest that both pair swimming and affiliative interaction were observed in generally fewer intervals during enrichment conditions when compared to baseline conditions, with an increase in interactions observed

during Enrichment 3 (Figure 3). After Enrichment 3, during Baseline 4, affiliative behavior dropped back to lower levels similar to earlier conditions, although pair swimming increased further. In summary, Enrichment 3, the session in which the most novel forms of enrichment were used, was associated with an increase in non-circle swimming, as well as pair swimming and affiliative behavior.

Figure 3

Percentage of Intervals that were Coded as Pair Swims and those that included Affiliative Behavior between the Two Dolphins over the Baseline and Enrichment Conditions in Experiment 1



Note. This graph illustrates general trends, as the differences were not significant

Experiment 2

Method

The purpose of Experiment 2 was to explore the premise that allowing a dolphin to choose an object as opposed to providing them with a predetermined enrichment item would increase the dolphin’s engagement with that object and promote affiliative interaction with other dolphins and trainers.

Subjects

Apollo, an approximately three-year-old male bottlenose dolphin, was the main participant in Experiment 2. However, another young dolphin (Chance, approximately four years old) was also present in the enclosure, along with Bo and Buster. Both Apollo and Chance had been stranded along the Gulf Coast and were deemed nonreleasable due to the extent of their injuries upon stranding. Following standard precautionary measures, Chance and Apollo were initially kept in quarantine for several months, where they had been physically, but not acoustically, separated from Bo and Buster in a separate pool. When each dolphin was permanently assigned, they were moved into the main pool complex where they could see and hear Bo and Buster through a net barrier but could not initially physically interact. As a result, all four animals had only been able to swim freely with one another for approximately two weeks before the time of the experiment. While Apollo was the only dolphin involved in the choice training experiment (i.e., the only dolphin who could make a choice), the other three dolphins were in the same pools had therefore had access to Apollo and to the enrichment items once they were placed in the pools.

Pre-Experimental Training

Training of the choice behavior was conducted up to two times per day at the end of each regular training session, while the animal was still at station. To train this behavior, the trainer held two enrichment objects, one to the left and one to the right of the dolphin. In order to shape the choice behavior, the objects were first presented ~6 in. on either side of the dolphin’s rostrum. If the

dolphin touched an object, that object was added to the pool. As the training progressed, the objects were gradually moved to a distance of 12 in. on either side of the rostrum, requiring exaggerated movement from the animal in order to select an enrichment item. Once the animal touched an object, the behavior was not bridged or reinforced in any way, other than placing the selected item into the pool water next to the dolphin.

A total of 32 training trials were conducted over a period of two and a half weeks. A total of 16 possible standard enrichment items were used during training. The presentation of items was pseudorandomized and balanced for the number of times each object was presented to the right or the left. No object was presented more than four times throughout the training period, and unique object pairings were used in each training session. Training of the choice behavior was considered complete when the subject completed all 32 trials and had consistently chosen objects without bias for a specific side (left or right). Apollo was the only animal to successfully complete choice training and therefore was the only animal to participate in experimental trials.

Experimental Conditions





The experiment included three conditions, a baseline condition followed by two experimental conditions (i.e., choice and nonchoice), which were alternated each day. Each condition lasted a total of five days. The baseline condition included only standard enrichment items (a random assortment of 12 items that included various floats, balls, and hoops). Apollo (as well as the other dolphins) had a minimum of one month of previous experience with these items prior to the experiment.




For treatment conditions, 15 novel objects were used as enrichment items (Table 3). For both choice and nonchoice trials, the order in which objects were presented were pseudorandomized based on the size of the object (large or small) and the presence or absence of dangling a heavy-duty felt material, designed to resemble kelp, which had been suggested by the trainers to be one of Apollo’s preferred materials. For choice trials, object pairings were also pseudorandomized according to the side on which each object type was presented.

Ten trials (five choice and five nonchoice) were run across nonconsecutive days with one trial each day. For the nonchoice condition, at the end of the training session, a novel enrichment item (chosen by the randomization schedule) was shown to the dolphin and then immediately placed in the pool and, following standard procedure, left in the pool overnight until the next training session (approximately 8-10 hr). For choice conditions, the dolphin was presented with two novel objects from which to choose. The first object that was touched by the dolphin was considered to be the choice and was immediately placed in the pool. The dolphin received no other rewards for choosing the item, and the session was ended without further reinforcement.

Table 3

Enrichment Items Used in Each Trial of Experiment 2

Trial	Left Hand	Right Hand	Apollo	
1	NON-CHOICE 			
2	NOODLE W/KELP SQUARES NON-CHOICE  FLOATING HOSE			
3	JOLLYBALL 	BOOGIE BOARD 	L	R

4	<p style="text-align: center;">BAT</p> 	<p style="text-align: center;">SMALL NOODLE RING</p> 	L R
5	<p style="text-align: center;">NON-CHOICE</p>  <p style="text-align: center;">SINKING HOSE</p>		

Data Collection

Behavioral observations were recorded twice each day and focused on Apollo. The only data collected for other dolphins occurred when Apollo was engaged with them (pair swimming, affiliative and agonistic behavior, interference). The first observation occurred immediately following the training session, and the second occurred during a pre-determined, randomly selected timeslot later in the day. Behavioral observations followed the procedure described for Experiment 1. To clarify the difference between circle and non-circle swimming, the behavioral ethogram for Experiment 2 was modified to ensure that pair swims were no longer mutually exclusive but were considered a modifier to the other swim types. A few additional behaviors were also added. Affiliative activity was expanded to include group swimming, orienting toward another dolphin, touching another dolphin, chase/following, flee/avoidance, tooth raking, and chin or tail slapping. Interference was defined as one dolphin moving between another dolphin and the toy with which they were interacting. Interference most often resulted in blocking another dolphin’s access to a desired object and, similar to displacement behaviors, would be considered agonistic.

Data Analysis

Because there were far fewer sessions in Experiment 2, nonparametric analyses were conducted on total frequencies of intervals within session types. Chi-Square tests for independence determined whether behavioral patterns were similar between condition types.

Results

Apollo was the focus of our study, so, unless otherwise noted, these results refer to his behavior. Swim behavior (circle, non-circle, and stationary) differed between experimental and baseline conditions, $X^2(2, N = 450) = 39.50, p < .01$, and between choice and non-choice conditions, $X^2(1, N = 300) = 17.70, p < .01$). Circle swimming decreased during experimental conditions (11 intervals during baseline vs. 0 intervals during experimental), while non-circle swimming increased (95 intervals during baseline vs. 109 during non-choice and 137 during choice), suggesting that novel enrichment items had the intended result of increasing behavioral flexibility. The frequency of non-circle swimming was slightly higher during the choice condition than the non-choice condition, nearing significance, $X^2(1, N = 246) = 3.19, p = .07$.

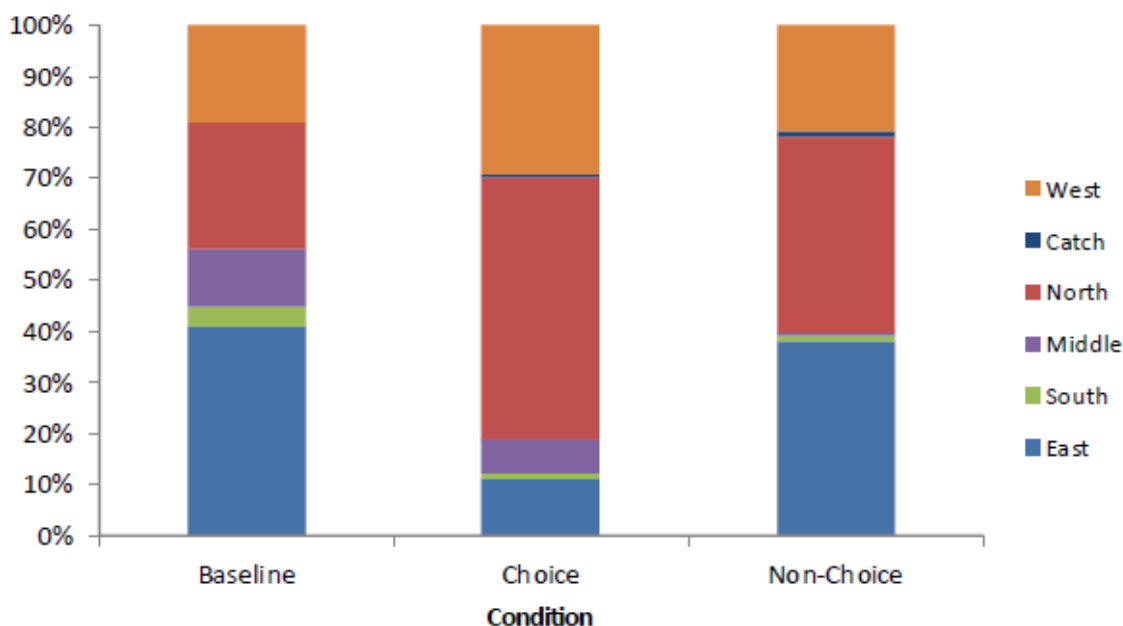
Interaction with standard enrichment objects remained relatively stable ($M = 60$ occurrences per condition) across baseline and treatment conditions, $X^2(2, N = 179) = 0.58, p = .89$. However, Apollo played with objects significantly less in the choice condition versus the nonchoice condition when novel and standard objects were combined (65 intervals vs. 106 respectively, $X^2(1, N = 171) = 9.83, p < .01$). This difference was driven by Apollo’s tendency to play less with the novel objects but only when he had chosen them. There was no significant difference between play with novel objects and play with standard enrichment objects during the non-choice condition (53 vs. 60 occurrences), $X^2(1, N = 187) = 0.43, p < .05$. However, during the choice condition, object play with novel objects decreased by over two-thirds (17 vs. 57 occurrences), $X^2(1, N = 187)$

= 21.60, $p < .05$). Because these results were contrary to the hypothesized outcome, additional analyses were conducted to create a clearer understanding of other behavioral changes that were brought about during the choice condition.

Importantly, Apollo also exhibited a significant change in habitat usage across five of the six pool areas when baseline, choice, and nonchoice conditions were compared (Figure 4), $\chi^2(8, N = 397) = 76.50, p < .01$. Apollo spent less time in the main pool areas (East and West) during the choice condition (40% of intervals), when compared to both the baseline and nonchoice conditions (60%).

Figure 4

Shift in Habitat Usage (Percentage of Intervals in each Pool) during Each Condition of Experiment 2



In addition, there was a positive correlation between interference from Chance and object play in both choice, $r(150) = 0.32, p < .01$, and nonchoice treatments, $r(150) = 0.21, p < .01$. Chance did not interfere during the baseline condition nor did the older dolphins interfere in any condition. Additionally, combined affiliative activity for all animals was less frequent during experimental conditions compared to baseline (82 intervals) and was less frequent during the choice condition (27 intervals) than the nonchoice condition (57 intervals), $\chi^2(2, N = 166) = 27.41, p < .001$. These results suggest that Chance interfered with Apollo, shifting Apollo's pool usage and contributing to his decrease in affiliative activity and object play when novel enrichment was present, particularly during the choice condition.

Discussion

In both experiments, enrichment objects provided the predicted increase in behavioral flexibility, as measured by an increase in non-circle swimming (and therefore a decrease in ISP). It is important to note that this increase does not immediately indicate an increase in animal welfare, and further examination of the data bears out that concern. The decrease in ISP was strongest when the enrichment devices were highly novel, large, and potentially even disruptive. For example, one of the most effective enrichment devices was a large block of ice (trash can sized). The dolphins initially reacted by avoiding the ice, pair swimming, and increasing affiliative interaction with each other, only later approaching the cube. These kinds of disruptions can be beneficial, as they break up potential boredom routines, but disruptions may not be preferable as regular

enrichment, as they could potentially provoke stress. Similar devices would need to be further tested with biological measures of stress to determine their benefits.

Other, less dramatic enrichment was sometimes accompanied by other behavioral shifts which were unintended and often not necessarily desirable. These behavioral shifts included a decrease in pair swimming and affiliative behavior in Experiment 1 (Enrichment Conditions 1 and 2) and an increase in interference (similar to displacement from a desired object and an agonistic behavior) in Experiment 2. These unintended consequences underscore the need for consistent and repeated monitoring of enrichment programs for animals in human care.

Interestingly, these seemingly desirable behavioral changes were not accompanied by an increased interaction with the enrichment devices. Instead, the dolphins altered their movements to exclude the areas where the enrichment was present, likely due to the increased novelty of the items (Kuczaj et al., 2002; Neto et al., 2016). It is also possible that with a longer habituation phase, the dolphins may have begun to approach and interact with the novel items, and the resultant behavioral changes may or may not have been maintained. Although shorter enrichment periods are typically considered best because they reduce habituation and maintain the novelty of the enrichment (Kuczaj et al., 2002), in this case, signs of habituation were not observed even with enrichment times of up to 8 hr.

Although these experiments were designed as a short-term assessment of environmental enrichment in inducing behavioral change, the short duration of each condition and subsequent break in between conditions may have inadvertently increased the effectiveness of enrichment as a whole, as changes to schedules and different timing can have strong effects on the effectiveness of enrichment (Fisher, 2005; Lacinak et al., 1999). That is, the dolphins may have been influenced by the cumulative effect of using multiple forms of novel enrichment in a relatively short period of time.

Of interest is the fact that choice (which was hypothesized to provide some form of perception of control – at minimum, control over the type of enrichment provided) in Experiment 2, did not result in the expected increase in affiliative social activity but rather produced a spike in agonistic behavior from the other young dolphin in the environment. This outcome was likely affected by the young age of the dolphin participant and the social structure, which was still most likely in a state of flux due to the introductions of the young animals to the group. It is possible that control is more effective when all animals are offered similar options rather than only one animal (and the youngest animal as well).

Also of note is the fact that there was more interference during the choice condition than the nonchoice condition, even though the kinds of objects that were added to the pool were similar. This may indicate that choice resulted in a change in behavior that was impactful enough to generate interest from another dolphin but was not observable by the researchers. We can say, however, that because Chance only showed increased interference when Apollo was given a choice, the dolphins clearly perceived the choice condition as different from the nonchoice condition.

These findings highlight the possibility that enrichment items and the way they are presented may alter social interactions and different individuals in unintended ways (Bayne, 2005; Nelson & Mandrell, 2005). This possibility is of importance, even given the small numbers of animals in these studies, because welfare concerns necessarily focus on individual responses rather than group averages. Smaller groups may even be more at risk of experiencing unintended consequences due to changes in enrichment. Unintended consequences such as fear, agitation, intergroup aggression, or other stress-related behaviors should always be of concern, particularly when the functional relevance of the enrichment is not taken into account (Newberry, 1995). Unintended consequences of enrichment can include within-group aggression and decreased habitat utilization (Lyn, 2009), as may have been seen in this study. Similarly, it is imperative to monitor the effects of enrichment over time, both short- and long-term. While the introduction of enrichment may initially reduce antagonistic behaviors, these behaviors may actually increase over time (Fisher, 2005).

Conclusions

While environmental enrichment is generally assumed to be of benefit to animals in human care, our results present a more complicated picture. Enrichment can certainly decrease unwanted behaviors, but, at least for cetaceans, those effects may be directly tied to the novelty of the enrichment devices (Makecha & Highfill, 2018; Shyne, 2006). In addition, adding novel enrichment frequently affects the social dynamics of a group, and these effects may be long-lasting (Lyn, 2009). Scientific assessment and frequent reevaluation of enrichment programs is strongly recommended.

Acknowledgments

Special thanks to the volunteers and interns who helped collect the data.

References

- Alliger, A. A., & Moller, P. (2011). The effects of environmental control on cognition in rats (*Rattus norvegicus*). *Journal of Applied Animal Welfare Science*, 14(4), 271–285. <https://doi.org/10.1080/10888705.2011.600153>
- Association of Zoos and Aquariums (2020). *Accreditation Standards*.
- Bayne, K. (2005). Potential for unintended consequences of environmental enrichment for laboratory animals and research results. *ILAR Journal*, 46(2), 129–139. <https://doi.org/10.1093/ilar.46.2.129>
- Bekoff, M., & Byers, J. A. (1992). Time, energy and play. *Animal Behaviour*, 44(5), 981–982. [https://doi.org/10.1016/S0003-3472\(05\)80593-7](https://doi.org/10.1016/S0003-3472(05)80593-7)
- Bloomsmith, M. A. A., Brent, L. Y. Y., & Schapiro, S. J. S. J. (1991). Guidelines for developing and managing an environmental enrichment program for nonhuman primates. *Laboratory Animal Science*, 41(4), 372–377.
- Blum, D. (2002). *Love at Goon Park: Harry Harlow and the science of affection*. Perseus Publishing.
- Brando, S., Broom, D. M., Acasuso-Rivero, C., & Clark, F. (2018). Optimal marine mammal welfare under human care: Current efforts and future directions. *Behavioural Processes*, 156, 16–36. <https://doi.org/10.1016/j.beproc.2017.09.011>
- Broom, D. M. (1988). The scientific assessment of animal welfare. *Applied Animal Behaviour Science*, 20(1–2), 5–19. [https://doi.org/10.1016/0168-1591\(88\)90122-0](https://doi.org/10.1016/0168-1591(88)90122-0)
- Broom, D. M. (2011). A history of animal welfare science. *Acta Biotheoretica*, 59(2), 121–137. <https://doi.org/10.1007/s10441-011-9123-3>
- Canali, E., & Keeling, L. (2009). Welfare quality project: From scientific research to on farm assessment of animal welfare. *Italian Journal of Animal Science*, 8(SUPPL. 2), 900–903. <https://doi.org/10.4081/ijas.2009.s2.900>
- Carlstead, K. (1991). Husbandry of the Fennec fox (*Fennecus zerda*) environmental conditions influencing stereotypic behaviour. *International Zoo Yearbook*, 30(1), 202–207. <https://doi.org/10.1111/j.1748-1090.1991.tb03487.x>
- Carlstead, K. (1998). Determining the causes of stereotypic behaviors in zoo carnivores: Toward appropriate enrichment strategies. In *Second nature: Environmental enrichment for captive animals* (pp. 172–183). Smithsonian Books.
- Clark, F. E. (2013). Marine mammal cognition and captive care: A proposal for cognitive enrichment in zoos and aquariums. *Journal of Zoo and Aquarium Research*, 1(1), 1–6. <https://doi.org/10.19227/jzar.v1i1.19>
- Clark, F. E., Davies, S. L., Madigan, A. W., Warner, A. J., & Kuczaj II, S. A. (2013). Cognitive enrichment for bottlenose dolphins (*Tursiops truncatus*): Evaluation of a novel underwater maze device. *Zoo Biology*, 32(6), 608–619. <https://doi.org/10.1002/zoo.21096>
- Clegg, I. L. K., Borger-Turner, J. L., & Eskelinen, H. C. (2015). C-Well: The development of a welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, 24(3), 267–282. <https://doi.org/10.7120/09627286.24.3.267>
- Clegg, I. L. K., & Delfour, F. (2018). Can we assess marine mammal welfare in captivity and in the wild? Considering the example of bottlenose dolphins. *Aquatic Mammals*, 44(2), 181–200. <https://doi.org/10.1578/AM.44.2.2018.181>
- Clegg, I. L. K., Van Elk, C. E., & Delfour, F. (2017). Applying welfare science to bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, 26(2), 165–176. <https://doi.org/10.7120/09627286.26.2.165>

- Daoudi, S., Badihi, G., & Buchanan-Smith, H. M. (2017). Is fixed-species living cognitively enriching? Enclosure use and welfare in two captive groups of tufted capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*). *Animal Behavior and Cognition*, 4(1), 51–69. <https://doi.org/10.12966/abc.05.02.2017>
- de Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science*, 102(3–4), 329–343. <https://doi.org/10.1016/j.applanim.2006.05.034>
- Delfour, F., & Beyer, H. (2012). Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology*, 31(2), 137–150. <https://doi.org/10.1002/zoo.20383>
- Delfour, F., Faulkner, C., & Carter, T. (2017). Object manipulation and play behavior in bottlenose dolphins (*Tursiops truncatus*) under human care. *International Journal of Comparative Psychology*, 30
- Eilam, D., Zor, R., Szechtman, H., & Hermesh, H. (2006). Rituals, stereotypy and compulsive behavior in animals and humans. *Neuroscience and Biobehavioral Reviews*, 30(4), 456–471. <https://doi.org/10.1016/j.neubiorev.2005.08.003>
- Eskelinen, H., Winship, K., & Borger-Turner, J. (2015). Sex, age, and individual differences in bottlenose dolphins (*Tursiops truncatus*) in response to environmental enrichment. *Animal Behavior and Cognition*, 2(3), 241–253. <https://doi.org/10.12966/abc.08.04.2015>
- Fernandez, E. J., & Timberlake, W. (2019). Foraging devices as enrichment in captive walrus (*Odobenus rosmarus*). *Behavioural Processes*, 168, 103943. <https://doi.org/10.1016/j.beproc.2019.103943>
- Fisher, G. (2005). *The effects of different levels of environmental enrichment on behavior in captive southern sea otters (Enhydra lutris nereis)*. Hunter College.
- Franks, B., Lyn, H., Klein, L., & Reiss, D. L. (2009). The influence of feeding, enrichment, and seasonal context on the behavior of Pacific Walrus (*Odobenus rosmarus divergens*). *Zoo Biology*, 28(3), 1–8. <https://doi.org/10.1002/zoo.20272>
- Greening, L. (2019). Stereotypies and other abnormal behavior in welfare assessment. In J. C. Choe (Ed.), *Encyclopedia of animal behavior* (Vol. 1, 2nd ed., pp. 141–146). Elsevier Academic Press. <https://doi.org/10.1016/B978-0-12-809633-8.90023-2>
- Gygax, L. (1993). Spatial movement patterns and behaviour of two captive bottlenose dolphins (*Tursiops truncatus*): Absence of stereotyped behaviour or lack of definition? *Applied Animal Behaviour Science*, 38(3), 337–344. [https://doi.org/https://doi.org/10.1016/0168-1591\(93\)90031-J](https://doi.org/https://doi.org/10.1016/0168-1591(93)90031-J)
- Hahn, N. E., Lau, D., Eckert, K., & Markowitz, H. (2000). Environmental enrichment-related injury in a macaque (*Macaca fascicularis*): Intestinal linear foreign body. *Comparative Medicine*, 50(5), 556–558.
- Hare, V. J., Rich, B., & Worley, K. E. (2007). Enrichment gone wrong! *Proceedings of the Eighth International Conference on Environmental Enrichment*, 35–45.
- Highfill, L. E., & Kuczaj II, S. A. (2007). Do bottlenose dolphins (*tursiops truncatus*) have distinct and stable personalities? *Aquatic Mammals*, 33(3), 380–389. <https://doi.org/10.1578/am.33.3.2007.380>
- Hosey, G., Melfi, V., & Ward, S. J. (2020). Problematic animals in the zoo: The issue of charismatic megafauna. In F. Angelici & L. Rossi (Eds.), *Problematic wildlife II*. Springer. https://doi.org/10.1007/978-3-030-42335-3_15
- Hoy, J. M., Murray, P. J., & Tribe, A. (2010). Thirty years later: Enrichment practices for captive mammals. *Zoo Biology*, 29(3), 303–316. <https://doi.org/10.1002/zoo.20254>
- Jaakkola, K., & Willis, K. (2019). How long do dolphins live? Survival rates and life expectancies for bottlenose dolphins in zoological facilities vs. wild populations. *Marine Mammal Science*, 35(4), 1418–1437. <https://doi.org/10.1111/mms.12601>
- Jones, B., Zapetis, M., Samuelson, M. M., & Ridgway, S. (2020). Sounds produced by bottlenose dolphins (*Tursiops*): A review of the defining characteristics and acoustic criteria of the dolphin vocal repertoire. *Bioacoustics*, 29(4), 399–440. <https://doi.org/10.1080/09524622.2019.1613265>
- Kuczaj, S., Lacinak, T., Trone, M., Solangi, M., & Ramos, J. (2002). Keeping environmental enrichment enriching. *International Journal of Comparative Psychology*, 15(2/3), 127–137.
- Lacinak, T., Turner, T. N., & Kuczaj, S. A. (1999). Training, enrichment, and behavior. In K. Ramirez (Ed.), *Animal training: Successful animal management through positive reinforcement* (pp. 269–271). Shedd Aquarium.
- Lyn, H. (2009). Are stereotypies always bad? Is enrichment always good? And how do we know? Paper presented at *International Marine Animal Trainers Association meeting*, Atlanta, GA.
- Makecha, R. N., & Highfill, L. E. (2018). Environmental enrichment, marine mammals, and animal welfare: A brief review. *Aquatic Mammals*, 44(2), 221–230. <https://doi.org/10.1578/AM.44.2.2018.221>
- Mason, G. J., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, 102, 163–188. <https://doi.org/10.1016/j.applanim.2006.05.041>
- Mason G. J. (1991). Stereotypies: A critical review. *Animal Behaviour*, 41, 1015–1037. [https://doi.org/10.1016/S0003-3472\(05\)80640-2](https://doi.org/10.1016/S0003-3472(05)80640-2)
- McPhee, M. E. (2002). Intact carcasses as enrichment for large felids: Effects on on- and off-exhibit behaviors. *Zoo Biology*, 21(1), 37–47. <https://doi.org/10.1002/zoo.10033>

- Mellen, J., & MacPhee, M. (2001). Philosophy of environmental enrichment: Past, present, and future. *Zoo Biology*, 20, 211–226. <https://doi.org/10.1002/zoo.1021>
- Miller, L. J. (2012). Visitor reaction to pacing behavior: Influence on the perception of animal care and interest in supporting zoological institutions. *Zoo Biology*, 31(2), 242–248. <https://doi.org/10.1002/zoo.20411>
- Miller, L. J., Kuczaj II, S. A., & Herzing, D. (2011). Stereotypic behavior in wild marine carnivores? *Zoo Biology*, 30(4), 365–370. <https://doi.org/10.1002/zoo.20347>
- Miller, L. J., Mellen, J. D., Greer, T., & Kuczaj, S. A. (2011). The effects of education programmes on Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour. *Animal Welfare*, 20(2), 159–172.
- Nelson, R. J., & Mandrell, T. D. (2005). Enrichment and nonhuman primates: “First, do no harm.” *ILAR Journal*, 46(2), 171–177. <https://doi.org/10.1093/ilar.46.2.171>
- Nelson Slater, M., & Hauber, M. E. (2017). Olfactory enrichment and scent cue associative learning in captive birds of prey. *Zoo Biology*, 36(2), 120–126. <https://doi.org/10.1002/zoo.21353>
- Neto, M. P., Silveira, M., & Dos Santos, M. E. (2016). Training bottlenose dolphins to overcome avoidance of environmental enrichment objects in order to stimulate play activities. *Zoo Biology*, 35(3), 210–215. <https://doi.org/10.1002/zoo.21282>
- Newberry, R. C. C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, 44(2–4), 229–243. [https://doi.org/10.1016/0168-1591\(95\)00616-Z](https://doi.org/10.1016/0168-1591(95)00616-Z)
- Pace, D. (2000). Fluke-made bubble rings as toys in bottlenose dolphin calves (*Tursiops truncatus*). *Aquatic Mammals*, 26(1), 57–64.
- Poirier, C., & Bateson, M. (2017). Pacing stereotypies in laboratory rhesus macaques: Implications for animal welfare and the validity of neuroscientific findings. *Neuroscience and Biobehavioral Reviews*, 83, 508–515. <https://doi.org/10.1016/j.neubiorev.2017.09.010>
- Pomerantz, O., Meiri, S., & Terkel, J. (2013). Socio-ecological factors correlate with levels of stereotypic behavior in zoo-housed primates. *Behavioural Processes*, 98, 85–91. <https://doi.org/10.1016/j.beproc.2013.05.005>
- Ramirez, K. (1999). *Animal training - Successful animal management through positive reinforcement*. Shedd Aquarium Press.
- Rumbaugh, D. M., Washburn, D., & Savage-Rumbaugh, S. (1989). On the care of captive chimpanzees: Methods of enrichment. In F. S. Evalyn (Ed.), *Housing, care and psychological wellbeing of captive and laboratory primates. Noyes series in animal behavior, ecology, conservation and management* (pp. 357–375). Noyes Publications.
- Samuelson, M. M., Lauderdale, L. K., Pulis, K., Solangi, M., Hoffland, T., & Lyn, H. (2016). Olfactory enrichment in California sea lions (*Zalophus californianus*): An effective tool for captive welfare? *Journal of Applied Animal Welfare Science*, 20(1), 1–11. <https://doi.org/10.1080/10888705.2016.1246362>
- Serres, A., Hao, Y., & Wang, D. (2020). Swimming features in captive odontocetes: Indicative of animals’ emotional state? *Behavioural Processes*, 170, 103998. <https://doi.org/10.1016/j.beproc.2019.103998>
- Shepherdson, D. J. (1998). Tracing the path of environmental enrichment in zoos. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 1–12). Smithsonian Institution Press.
- Shyne, A. (2006). Meta-analytic review of the effects of enrichment on stereotypic behavior in zoo mammals. *Zoo Biology*, 25(4), 317–337. <https://doi.org/10.1002/zoo.20091>
- Swaigood, R. R., & Shepherdson, D. J. (2005). Scientific approaches to enrichment and stereotypies in zoo animals: What’s been done and where should we go next? *Zoo Biol*, 24(6), 499–518. <https://doi.org/10.1002/zoo.20066>
- Ugaz, C., Valdez, R. A., Romano, M. C., & Galindo, F. (2013). Behavior and salivary cortisol of captive dolphins (*Tursiops truncatus*) kept in open and closed facilities. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8(4), 285–290. <https://doi.org/10.1016/j.jveb.2012.10.006>
- Wagman, J. D., Lukas, K. E., Dennis, P. M., Willis, M. A., Carroscia, J., Gindlesperger, C., & Schook, M. W. (2018). A work-for-food enrichment program increases exploration and decreases stereotypies in four species of bears. *Zoo Biology*, 37(1), 3–15. <https://doi.org/10.1002/zoo.21391>
- Waples, K. A., & Gales, N. J. (2002). Evaluating and minimising social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology*, 21(1), 5–26. <https://doi.org/10.1002/zoo.10004>
- Weiss, J. M. (1971). Effects of coping behavior with and without a feedback signal on stress pathology in rats. *Journal of Comparative and Physiological Psychology*, 77(1), 22–30. <https://doi.org/10.1037/h0031581>
- Wells, D. L. (2009). Sensory stimulation as environmental enrichment for captive animals: A review. *Applied Animal Behaviour Science*, 118(1–2), 1–11. <https://doi.org/10.1016/j.applanim.2009.01.002>
- Westlund, K. (2014). Training is enrichment-And beyond. *Applied Animal Behaviour Science*, 152, 1–6. <https://doi.org/10.1016/j.applanim.2013.12.009>
- Yeater, D. B., Miller, L. E., Caffery, K. A., & Kuczaj II, S. A. (2013). Effects of an increase in group size on the social behavior of a group of rough-toothed dolphins (*Steno bredanensis*). *Aquatic Mammals*, 39(4), 344–355. <https://doi.org/10.1578/AM.39.4.2013.344>

Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: June 14th, 2019
Resubmitted: October 5th, 2020
Accepted: October 5th, 2020