The University of Southern Mississippi The Aquila Digital Community

Dissertations

Spring 5-2017

Efficacy of Cognitive Enrichment for Bottlenose Dolphins (*Tursiops truncatus*): Evaluation of Planning Abilities Through the Use of a Novel Problem Solving Task

Lisa Kay Lauderdale University of Southern Mississippi

Follow this and additional works at: https://aquila.usm.edu/dissertations

Part of the Animal Studies Commons, Applied Behavior Analysis Commons, Experimental Analysis of Behavior Commons, Other Animal Sciences Commons, and the Zoology Commons

Recommended Citation

Lauderdale, Lisa Kay, "Efficacy of Cognitive Enrichment for Bottlenose Dolphins (*Tursiops truncatus*): Evaluation of Planning Abilities Through the Use of a Novel Problem Solving Task" (2017). *Dissertations*. 1399.

https://aquila.usm.edu/dissertations/1399

This Dissertation is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Dissertations by an authorized administrator of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

EFFICACY OF COGNITIVE ENRICHMENT FOR BOTTLENOSE DOLPHINS

(TURSIOPS TRUNCATUS): EVALUATION OF PLANNING ABILITIES

THROUGH THE USE OF A NOVEL PROBLEM-SOLVING TASK

by

Lisa Kay Lauderdale

A Dissertation Submitted to the Graduate School and the Department of Psychology at The University of Southern Mississippi in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

Dr. Stanley Kuczaj, Dissertation Director Professor, Psychology

Approved:

Dr. Donald Sacco, Committee Chair Assistant Professor, Psychology

Dr. Evan H. Dart, Committee Member Assistant Professor, Psychology

Dr. Richard S. Mohn, Committee Member Associate Professor, Educational Research and Administration

Dr. Lance J. Miller, Committee Member Senior Director, Animal Welfare Research, Brookfield Zoo, Chicago Zoological Society

Dr. D. Joe Olmi Department Chair, Psychology

Dr. Karen S. Coats Dean of the Graduate School

May 2017

COPYRIGHT BY

Lisa Kay Lauderdale

2017

Published by the Graduate School



ABSTRACT

EFFICACY OF COGNITIVE ENRICHMENT FOR BOTTLENOSE DOLPHINS (TURSIOPS TRUNCATUS): EVALUATION OF PLANNING ABILITIES THROUGH THE USE OF A NOVEL PROBLEM-SOLVING TASK

by Lisa Kay Lauderdale

May 2017

Environmental enrichment is a key component to improving the psychological and physiological well-being of animals in human care. Enrichment can be achieved through a variety of modalities, including the addition of objects and scents, or by providing the animals with additional challenges. The effectiveness of specific enrichment should be evaluated on a case-by-case basis to determine if the desired result is achieved. Environmental enrichment devices (EED's) can be utilized to present novel problems to animals in human care. When confronted with a novel problem, dolphins can plan their behavior to create a more efficient strategy than previously modeled.

The purpose of the present study was to investigate dolphins' ability to plan their behaviors using an interactive apparatus and accompanying weights and examine the enrichment value of the interactive apparatus. Two problems were presented to evaluate dolphins' ability to plan by collecting several weights at once, thus solving the apparatus more efficiently. In contrast to previous findings, dolphins in the present study failed to plan their behavior. Rather, individual differences in strategy and level of interaction with the apparatus arose throughout the experiment and are discussed here. The results indicate that the apparatus was engaging for some animals, evidenced by their continued interaction throughout the study, with or without reward. One dolphin continually solved the apparatus despite rarely consuming the food reward, suggesting that she was motivated to participate for the challenge itself. In contrast, another animal preferred to interact with the weights.

The presentation of the interactive apparatus may have resulted in small but measurable changes in behavior. There was a marginal effect of phase for behavioral diversity, with the highest behavioral diversity indices found in the treatment phase. Social swim states and usage of the bottom of the habitat were highest when the interactive apparatus was being presented. Combined, this suggests that the interactive apparatus may have resulted small changes in behavior.

ACKNOWLEDGMENTS

This dissertation would not have been possible without the guidance and expertise of my advisor, Dr. Stan Kuczaj, and my co-advisor, Dr. Lance Miller. I would like to thank Dr. Donald Sacco for chairing my committee and my committee members, Dr. Evan Dart and Dr. Richard Mohn. My sincerest thanks go to Rita Stacey and the Brookfield Zoo Seven Seas staff accommodating this project and for their insight and inspiration. I am incredibly appreciative of time and effort Dr. Melinda Conners spent completing reliability observations. Thank you to Dr. Mystera Samuelson for mastering the art of being a friend and mentor, and to Dr. Pepper Hanna and Audra Ames for the many writing sessions and problem-solving discussions. Finally, I would like to thank my lab mates and fellow graduate students for their professional and life assistance during the last four years.

DEDICATION

To my family ~ Thank you for your unwavering support and instilling the relentless desire to pursue my dreams.

TABLE OF CONTENTS

ABSTRACTii
ACKNOWLEDGMENTS iv
DEDICATION v
LIST OF TABLES ix
LIST OF ILLUSTRATIONS x
LIST OF ABBREVIATIONS xi
CHAPTER I – PLANNING IN THE BOTTLENOSE DOLPHIN (TURSIOPS
TRUNCATUS): AN EXAMINATION OF ABILITY, PARTICIPATION,
PREFERENCE, AND STRATEGY 1
Introduction1
Evolutionary Advantages to Planning 2
Variation in Planning Techniques and Skills2
Planning in Bottlenose Dolphins 4
Purpose of Study
Methods 6
Results
Group 1 10
Group 2 11
Discussion

Group 1	
Group 2	19
Conclusion	
CHAPTER II - EFFICACY OF AN INTERACTIVE APPARATUS AS COGNI	TIVE
ENRICHMENT FOR BOTTLENOSE DOLPHINS (TURSIOPS TRUNCATUS).	
Introduction	25
Indicators of Welfare	
Behavioral Diversity.	
Social Cohesion.	
Habitat Usage	
Challenging Enrichment Devices	
Choice and Control	
Habituation	
Purpose of Study	30
Methods	30
Results	
Behavior Data	
Swim State and Habitat Usage	
Discussion	41
Limitations	44

Conclusion	. 44
APPENDIX A – Swim State Operational Definitions	. 46
APPENDIX B – Location Operational Definitions	. 47
APPENDIX C – Behavior Event Operation Definitions	. 48
APPENDIX D – Behavior Categories	. 52
APPENDIX E – IACUC Approval Letter	. 53
REFERENCES	. 54

LIST OF TABLES

Table 1 Demographic information on participants	7
Table 2 Number of weights carried per 5-trial block	12
Table 3 Number of fish consumed per 5 trial block	13
Table 4 Demographic information on participants	31
Table 5 Mean Phase Behavioral Diversity Indices	37
Table 6 Mean Phase Swim State Diversity Indices	39
Table 7 Mean Phase Location Diversity Indices	40

LIST OF ILLUSTRATIONS

<i>Figure 1.</i> Location of apparatus and weights in the habitat7
<i>Figure 2.</i> Interactive apparatus
Figure 3. 1-lb and 3-lb weights
Figure 4. Graphs of the average number of weights carried per trial in each condition,
represented in 5-trial blocks
Figure 5. Graphs of the average number of fish consumed per trial in each condition,
represented in 5-trial blocks16
Figure 6. Graphs of the percentage of trials per block in which the 1-lb and 3-lb weights
were selected first, second, or third 17
Figure 6. Configuration of the Brookfield Zoo bottlenose dolphin habitat
Figure 7. Shannon-Weiner index values for behavioral diversity
Figure 8. Shannon-Weiner index values for each individual by phase
Figure 9. Shannon-Weiner index values for behavioral diversity by week
Figure 10. Mean proportion of time spent in a given swim state 40
<i>Figure 11</i> . Mean proportion of time spent in a given location

LIST OF ABBREVIATIONS

EED

Environmental Enrichment Device

CHAPTER I – PLANNING IN THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*): AN EXAMINATION OF ABILITY, PARTICIPATION, PREFERENCE, AND STRATEGY

Introduction

Planning has been defined as the ability to "represent and use causal knowledge to create solutions (novel or familiar) that are appropriate for achieving a specific goal in a particular problem environment" (Kuczaj, Gory, & Xitco, 2009, pp. 102). The ability to plan behavior flexibly is rare among non-human animals (Kuczaj, Makecha, Trone, Paulis, & Ramos, 2006; Reader & Laland, 2003). To plan a solution, an individual must understand the causal relations that are inherent to the problem (Gopnik & Schulz, 2007; Holyoak, 1995). Without causal understanding, no connection can be made between behavior and consequence (Holyoak, 1995). This causal understanding allows an individual to then determine why some efforts succeed and others do not, allowing he or she to avoid the potential consequences of error.

A crucial component of planning is the creation of novel behaviors in order to solve novel problems (Kuczaj et al., 2009). Planning-resultant behaviors should manifest themselves quickly and entirely when compared to solutions created over time via associative learning or through the accidental discovery of the correct solution (Frye, Zelazo, Brooks, & Samuels, 1996). In order to be successful at planning, individuals must be able to mentally represent the problem and determine the desired outcome (Gopnik & Schulz, 2007; Hauser, Kralik, & Botto-Mahan, 1999; Procyk & Joseph, 1996; Tolman, 1932; Washburn, 1936). Additionally, animals must have the ability to mentally represent

1

possible solutions that would achieve the desired outcome and to manipulate these representations (Piaget, 1955).

Evolutionary Advantages to Planning

Generalized planning abilities may have provided an evolutionary advantage to some species by allowing individuals to actively respond to their environment by planning their behavior rather than passively reacting (Tolman, 1932). In the wild, animals will regularly encounter a variety of complex social and physical situations in which the ability to plan behavior facilitates an individual's ability to adapt and thrive (Miyata & Fujita, 2012; Reader & Laland, 2003).

The ability to plan behavior and forecast the possible reactions of conspecifics before acting is beneficial for highly social species (Barth, Povinelli, & Cant, 2004; Povinelli & Cant, 1995). In social non-human primate species living in fission-fusion societies, inhibitory skills are more prevalent and are suggested to be a result of the need to assess the composition of the party prior to action (Amici, Aureli, & Call, 2008). Similarly, bottlenose dolphins (*Tursiops truncatus*) typically live in fission-fusion societies (Connor, Wells, Mann, & Read, 2000; Gowans, Würsig, & Karczmarski, 2007) in which the ability to assess the situation and the other individuals present may be crucial.

Variation in Planning Techniques and Skills

The diversity of situations in which planning skills are expressed is cited as a crucial difference between human and non-human planning (Gilbert & Wilson, 2007; Roberts, 2012; Suddendorf & Corballis, 2007). There is significant variation in the capacity to plan physical actions between and within species as well, based on the type of

task to be solved (D'Mello & Franklin, 2011; Völter & Call, 2012). Great apes have been documented saving tools for future use (Dufour & Sterck, 2008; Mulcahy & Call, 2006; Osvath & Osvath, 2008) and for use as projectiles (Osvath, 2009; van Hooff & Lukkenaar, 2015), indicating basic planning skills, yet the diversity of the species' planning abilities has only recently been explored utilizing cognitive research techniques (Bourjade, Call, Pelé, Maumy, & Dufour, 2014; Tecwyn et al., 2012).

Recent research has focused on great apes' abilities to plan outside of tool use. Bourjade and colleagues (2014) presented Sumatran orangutans (*Pongo abelii*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*) with a token exchange task and manipulated conditions to investigate if individuals could modify their plans to suit future needs. All three species were capable of planning when required to transport valuable and non-valuable tokens to different rooms. However, a high level of variability within planning responses existed across species. For example, orangutans attended to the temporal components of the task more so than the other species and were fairly unselective in choosing tokens with value, chimpanzees were more selective in choosing valuable tokens than the other species, and bonobos adjusted to the experimental conditions quickly and were more apt to select valuable tokens but only when they would needed in the future (Bourjade et al., 2014).

Two out of three orangutans (*Pongo spp.*) were able to solve a trial-unique puzzle task by choosing the correct path when presented with two paths with multiple obstacles (Tecwyn, Thorpe, & Chappell, 2012). These results suggested that the subjects could consider some of or all the obstacles to receive the reward, indicating that they may have planned for the obstacles prior to execution. Further investigation by Tecwyn and colleagues provided evidence that Bornean orangutans (*Pongo pygmaeus*) and bonobos were unable to solve a three-level paddle box problem, which required them to move one or two, lower-level non-reward paddles before moving the top-level paddle with the reward on it (Tecwyn et al., 2013). The experiment required them to both inhibit the response of moving the paddle with the reward first and plan the direction in which the reward would fall by changing the paddles beneath it. However, in a follow-up experiment, both bonobos and orangutans could plan their behavior to solve the same paddle task when they were able to move the paddle with the reward first and then solve the lower levels sequentially (Tecwyn et al., 2013).

Planning in Bottlenose Dolphins

Observations of wild dolphin behavior suggest that they may implement plans in a variety of contexts. Specifically, cooperation during mate acquisition and foraging/hunting techniques provides evidence that dolphins may engage in planning (see Kuczaj et al., 2009; Kuczaj & Walker, 2012 for a review of potential planning behavior of cetaceans in the wild and under human care). However, it is important to note that investigating the planning abilities of wild dolphins is particularly difficult because the full learning history of the individual of interest is unknown (Kuczaj et al., 2009). Therefore, dolphins under human care make excellent research participants because the behavior and experiential history of the animal is known and new problems can be created.

Research at Disney's The Living Seas revealed that bottlenose dolphins were able to create a simple plan in order to solve an apparatus (Kuczaj, Xitco, & Gory, 2010). The dolphins were given one weight and presented with several boxes that allowed the weight to fall through and one box that retained the weight. To maximize the number of fish they would receive, the dolphin needed to use all the boxes that allowed the weight to fall through first and drop the weight into the retaining box last. Both subjects arrived at the correct solution independently, indicating that they could create and follow a rudimentary plan.

Kuczaj et al. (2009) used a multiple weight apparatus to evaluate if dolphins can plan future behaviors to obtain a reward. The dolphins were required to place the weights inside the apparatus, designed to release a food reward when triggered by four weights. The weights consisted of weighted cylinders of PVC pipe with a connected ring. They were placed at varying distances around the apparatus. Scuba divers modeled a method to solve the apparatus by placing each weight into the apparatus one at a time. In the near condition, the dolphins completed the behavior by retrieving one weight at a time as modeled by the divers. As it was likely that the dolphins simply did not have an incentive to modify the plan to create a more efficient method because the weights were close to the apparatus, the researchers moved the weights farther away from the apparatus for the far condition. The dolphins quickly devised a novel solution; they retrieved multiple weights at a time, thus solving the puzzle with greater efficiency than was modeled. The immediate change in weight retrieval method suggested that the dolphins could create a rudimentary plan to solve the task and were responding to changes in their environment. Hence, it can be hypothesized that they may have the ability to update their plans based on the resources available.

5

Purpose of Study

The purpose of the present study was to investigate dolphins' ability to plan their behaviors using a submerged interactive apparatus. Building on the work of Kuczaj and colleagues (2009), two problems were presented, with the end goal of examining if dolphins could plan ahead by collecting several weights at once and if they could monitor and modify their planned behavior-based the resources available. The first problem replicated the scenario presented to the dolphins by Kuczaj and colleagues and the second problem introduced new features to the previous scenario.

The following research questions were examined: (1) Can dolphins plan their behavior to solve a novel problem?; and (2) Can dolphins update their plan based on the available resources? It was hypothesized that the dolphins would plan their response by creating a new behavior (i.e., carrying multiple weights at one time) to solve the apparatus for problem 1. It was hypothesized that the dolphins would modify their behavior to carry fewer, 3-lb weights rather than more, 1-lb weights for problem 2.

Methods

Eight Atlantic bottlenose dolphins (*Tursiops truncatus*), housed at the Brookfield Zoo in Brookfield, Illinois, USA were exposed to an underwater interactive apparatus designed to investigate their ability to plan behavior over a 4-month period. Group 1 consisted of three sub-adult females and one male calf, and Group 2 consisted of one female/male mother-calf dyad and one female/female mother-calf dyad (Table 1). The enclosure consisted of four interconnected pools: an oblong front pool (33.5 m across, 12.2 m wide, and 6.7 m deep), two circular rear pools (10.7 m diameter, 4.3 m deep), and a medical pool (7.6 m diameter, 2.4 m deep; Figure 1).

Table 1

Demographic information on participants

Dolphin	Age	Group	Sex
Dolphin 1	30	2	Female
Dolphin 2	11	1	Female
Dolphin 3	2	2	Male
Dolphin 4	1	1	Female
Dolphin 5	2	2	Male
Dolphin 6	13	1	Female
Dolphin 7	14	1	Female
Dolphin 8	34	2	Female



Figure 1. Location of apparatus and weights in the habitat.

The dolphins received their regular training sessions and normal daily allotment of food throughout the data collection process. The interactive apparatus (Figure 2) consisted of a clear Lexan box, submerged two feet beneath the water's surface, containing a shelf that was lowered to release a food reward (four fish) when a given amount of weight (Figure 3) was placed inside. Trials were conducted five days a week between 1200 and 1300, directly following a training session in which they were fed. Therefore, the reward acted as an indicator that the correct solution had been found rather than a method of food distribution. The trials were recorded from above the water using a Canon Powershot S110 video camera and from two GoPro Hero, 4 Sessions mounted in stationary positions inside apparatus. Dolphins were introduced to the 1-lb weights as retrieval objects during training sessions before the baseline phase and were naïve to the apparatus at the beginning of the baseline phase.

In each trial, the weights were dropped into the water in a specified location (Figure 1) and then the apparatus was lowered into position on the back wall where the dolphins had the opportunity to solve it. The dolphins were presented trials with the weights in three different configurations. Condition 1 was comprised of 25 trials, condition 2 was comprised of 25 trials, and condition 3 was comprised of 30 trials. The apparatus was placed in the back pools in all conditions and the location and type of weight varied based on the condition. The weights were placed on the opposite side of the back pool for the baseline phase, modeling phase, and condition 1 and in the front pool in condition 2 and condition 3 (Figure 1). The baseline phase was counterbalanced between Group 1 and Group 2. For Group 1, the apparatus was placed into the water, with no weights, for 20 minutes a day, for three days. Both the apparatus and the weights were then placed into the water for 20 minutes a day, for three days. For Group 2, the apparatus and the weights apparatus and the weights were placed into the water for 20

minutes a day, for three days. Next, the apparatus was placed into the water without weights, for 20 minutes a day, for three days.



Figure 2. Interactive apparatus.

The 'Closed' apparatus is in the pre-trial position without weights resting on the shelf. The 'Semi-open' apparatus is mid-trial with two 1-lb weights partially depressing the shelf. The 'Open' apparatus is post-trial with three 1-lb weights fully depressing the shelf.



Figure 3. 1-lb and 3-lb weights.

The photo on the left depicts the red, 1-lb weight. The photo on the right depicts the yellow, 3-lb weight.

In the modeling phase for condition 1, the trainer modeled the act of putting a single 1-lb weight in the apparatus. Upon the third weight, four fish were released from

the apparatus. The apparatus was reset and the dolphins were given five minutes to solve the apparatus. Condition 1 began after the dolphins solved the apparatus on their own three times. Condition 1 was comprised of 25 trials, condition 2 was comprised of 25 trials, and condition 3 was comprised of 30 trials.

In condition 1, six 1-lb weights were placed on pool floor on the opposite side of the back pool from the apparatus. If the dolphins did not interact with the apparatus for five consecutive minutes, the apparatus was removed from the pool. Three weights were required to solve the apparatus. In condition 2, the apparatus remained in the same position in the back pool and the six 1-lb weights were moved into the front pool, farther away from the apparatus. Three weights were still required to solve the apparatus.

Trainers introduced the yellow, 3-lb weights as retrieval objects before condition 3 began. The dolphins never observed a trainer solving the apparatus with the 3-lb weight. In condition 3, four 1-lb weights and two 3-lb weights were placed in the front pool. The apparatus could be solved with three 1-lb weights, one 3-lb weight, or any combination of the two with the 3-lb weight releasing the food reward.

Results

Group 1

Group 1 included three sub-adult females (Dolphin 2, Dolphin 6, and Dolphin 7) and one male calf (Dolphin 3). At the end of the modeling phase, Dolphin 7 retrieved two weights in one trip and placed them both in the apparatus. However, due to three unintended deployments of the food reward on at the beginning of condition 1, Group 1 returned to and remained in the modeling phase for the duration of the testing period. On the first trial of condition 1, Dolphin 6 placed one weight on top of the apparatus, near the opening. Dolphin 6 then moved near the location where the food reward was released and nudged the apparatus with her rostrum. This caused the weight to fall in and the fish to be released. After this trial, she adopted pushing the apparatus as a problem-solving strategy. Pushing the apparatus caused the moving water to lower the shelf and release the fish. The other female dolphins in the group modeled Dolphin 6 and adopted this strategy as well. To mitigate this issue, the apparatus was modified to include a hidden lever that allowed the researcher to manually release the fish upon the third weight. Despite the modification, the pushing strategy persisted for the three females, and the male calf did not interact with the apparatus.

In addition to pushing, Dolphin 2, Dolphin 6, and Dolphin 7 developed two other strategies in their attempts to obtain the food reward in addition to pushing. They began using a tail-swishing action and a head-swishing action, in which they quickly moved water with their flukes or head towards the apparatus, without making contact.

Group 2

Group 2 included two adult females, Dolphin 1 and Dolphin 8, and their calves, Dolphin 4 and Dolphin 5, respectively. All the dolphins participated in a minimum of two trials. One individual participated or solely solved every completed trial (Figure 4). Of the 168 weights placed in the apparatus, Dolphin 4 added 153. Despite solving most the trials, Dolphin 4 rarely consumed any of the food reward. She consumed 14 of 216 available fish, with only one fish consumed in condition 1 and 2 (Figure 5). Dolphin 8 added 9 of the 168 weights over the three conditions and consumed 162 fish. Dolphin 1 added two weights and consumed 40 fish. Dolphin 5 added four weights and did not consume any of the food reward. The results have been condensed into 5-trial blocks for

11

tables and figures. Table 2 shows the number of weights added in each condition (represented in 5-trial blocks) by individual and Table 3 shows the number of fish consumed by individual in each condition.

Table 2

Condition	Block	Dolphin 1	Dolphin 4	Dolphin 5	Dolphin 8
Condition 1	Block 1	1	11	2	1
	Block 2	0	10	1	1
	Block 3	0	12	0	0
	Block 4	0	13	0	0
	Block 5	1	14	0	0
Condition 2	Block 1	0	11	0	0
	Block 2	0	3	1	0
	Block 3	0	9	0	1
	Block 4	0	8	0	1
	Block 5	0	13	0	0
Condition 3	Block 1	0	7	0	0
	Block 2	0	10	0	1
	Block 3	0	9	0	1
	Block 4	0	8	0	0
	Block 5	0	8	0	2
	Block 6	0	7	0	1

Number of weights carried per 5-trial block

Table 3

Condition	Block	Dolphin 1	Dolphin 4	Dolphin 5	Dolphin 8
Condition 1	Block 1	0	1	0	19
	Block 2	0	0	0	16
	Block 3	8	0	0	4
	Block 4	0	0	0	16
	Block 5	6	0	0	14
Condition 2	Block 1	0	0	0	8
	Block 2	0	0	0	0
	Block 3	8	0	0	0
	Block 4	4	0	0	0
	Block 5	5	0	0	11
Condition 3	Block 1	0	3	0	13
	Block 2	0	0	0	20
	Block 3	2	2	0	12
	Block 4	3	4	0	5
	Block 5	4	4	0	8
	Block 6	0	0	0	16

Number of fish consumed per 5 trial block

Levels of participation varied between the participants, with Dolphin 4 adding weights in 90% of the trials, Dolphin 8 adding weights in 11% of the trials, Dolphin 5 adding weights in 5% of the trials, and Dolphin 1 adding weights in 3% of the trials. Condition 1, block 1 was the only block in which all for dolphins participated (Figure 4). There were four unsolved trials in condition 1, 16 unsolved trials in condition 2, and six unsolved trials in condition 3. Of these, one trial in condition 1, three trials in condition 2, and three trials in condition 3 had no weights placed in the apparatus. Three-pound weights were the first selected the most in block 6, however, 1-lb weights were continually used (Figure 6). The 3-lb were selected first in 25.9% of the trials, second in 42.1% of the trials, and third in 50% of the trials.

Dolphin 4's strategy for solving the apparatus was similar to the method modeled, by dropping, pushing, or tossing the weight into the hole at the top of the apparatus. Dolphin 8 and Dolphin 1 periodically added weights by dropping them in but never completed trials on their own. Instead, Dolphin 8 typically remained in the vicinity of the apparatus and approached when Dolphin 4 arrived with a weight. Dolphin 1 either remained near the apparatus when Dolphin 4 was retrieving weights within the same pool or followed Dolphin 4 into another pool while she was retrieving the weights. Nonaggressive displacement sometimes occurred depending on who was closest to the food reward. Food was consumed first by Dolphin 8, followed by Dolphin 1 and then Dolphin 4. No mother-calf food sharing was observed between Dolphin 1 and Dolphin 4.



Figure 4. Graphs of the average number of weights carried per trial in each condition, represented in 5-trial blocks.



Figure 5. Graphs of the average number of fish consumed per trial in each condition, represented in 5-trial blocks.



Figure 6. Graphs of the percentage of trials per block in which the 1-lb and 3-lb weights were selected first, second, or third.

Discussion

Overall, the apparatus was engaging for dolphins, as demonstrated by their continual interaction with it across 80 trials. They all regularly interacted with the apparatus by actively solving it, or watching others solve it. Although Kuczaj et al. (2009) found that dolphins planned their behavior on a very similar task, the dolphins participating in the present study did not follow the same pattern. The difference in behavior may be due to previous experience. That is, the dolphins who participated in the study by Kuczaj and colleagues had consistently participated in research projects involving different types of apparatuses, while the current participants did not. Below is a discussion of planning abilities, participation, preference, and strategy.

Group 1

Dolphin 7 retrieved two weights simultaneously and placed them both in the apparatus at the end of the modeling phase. Dolphin 7 did not have the opportunity repeat this strategy, however, the rapid change in strategy is reminiscent of the immediate change to a multiple weight strategy by the dolphins in the study by Kuczaj and colleagues. Unfortunately, without further trials, it is impossible to determine if Dolphin 7's multiple weight strategy would have persisted.

Even though they did not solve the apparatus, Dolphin 6 developed a "pushing" strategy that was initially successful at obtaining the food reward. Once pushing the apparatus failed to release the food reward, Dolphin 2, Dolphin 6, and Dolphin 7 implemented two other strategies, tail swishing, and head swishing. Clark, Davies, Madigan, Warner, & Kuczaj (2013) reported a similar "tail-beating" behavior of a dolphin in response to a challenging underwater maze device, suggesting that this may be a common problem-solving strategy among dolphins.

Group 2

The level of participation varied among the dolphins, as they had the choice to interact with the apparatus and the weights. Dolphin 5 interacted with the apparatus the least, adding only four weights, and never consuming any of the food reward. However, he regularly carried and played with the weights. Dolphin 1 and Dolphin 8 added single weights periodically throughout the trials and regularly consumed the food reward when Dolphin 4 solved the trials. Dolphin 4 consistently solved the apparatus without regularly receiving the food reward. However, the food reward may have acted as an indication the problem had been completed. Continual interaction suggested that the apparatus was still engaging despite the most of the group's failure at solving the problem (Swaisgood et al., 2001). Individual variations in the levels of engagement with free choice enrichment are consistent with prior reports of dolphin interactions with environmental enrichment devices (EED's; Delfour & Beyer, 2012; Kuczaj et al., 2002). The degree of interaction depends on the audience, as not all objects are equally engaging to dolphins of different ages and sexes (Eskelinen, Winship, & Borger-turner, 2015; Neto, Silveira, & dos Santos, 2016).

Play provides important opportunities for cognitive development in dolphins, especially calves, by allowing them to create innovative behaviors and practice locomotor skills (Kuczaj & Eskelinen, 2014). Burghardt (2005) defined five criteria for identifying play behaviors, each of which were present when Dolphin 4 was solving the apparatus. Dolphin 4 did not regularly consume the food reward, suggesting that solving the apparatus was self-reinforcing. She did not add weights to the apparatus in a stereotyped manner and these behaviors were sometimes exaggerated. Methods for adding the weights included behaviors such as directly dropping them in the apparatus, placing them on top and then pushing them in, and throwing them from afar. Finally, these behaviors were initiated when she was well fed and under relaxed conditions, suggesting that Dolphin 4 may have been engaging in play when interacting with the apparatus.

Participation decreased during condition 2 after the weights were moved farther away. Dolphin 4 solved the apparatus fewer times and ignored the apparatus more often, and Dolphin 8 consumed fewer of the rewards because she was not present when the fish were released (e.g., she left the apparatus and was swimming in another pool). Dolphin 1's reward consumption increased as she only consumed the food reward when Dolphin 8 was not present. The decreased participation from Dolphin 4 may have been due to the increased effort required to solve the apparatus or due to habituation to it. Additionally, Dolphin 4 may have been unable to finish the trials because the weights and the apparatus were in separate pools. As a calf, Dolphin 4 is not an autonomous individual and her movements were closely supervised by her mother, Dolphin 1. Dolphin 1 may have prevented her from switching pools multiple times in such a short time period.

Interest increased with the introduction of the 3-lb weights in condition 3. Through this introduction, new EED's were added to the environment, and when the apparatus released the fish became variable. Variable presentation of EED's maintains interest for longer periods of time (Delfour & Beyer, 2012), and devices that can be controlled or manipulated are more resistant to habituation (Markowitz & Line, 1989). Dolphin 4 solved these trials at a higher rate than in condition 2 and Dolphin 8 returned to the apparatus to receive most the food reward. Although the weights remained in the far location, fewer weights were needed to solve the apparatus. Trials were solved with less than three weights in 70% of the completed trials in condition 3. Therefore, Dolphin 4 had to switch pools less often to solve the apparatus than in condition 2.

Dolphin 4 consistently solved the apparatus without regularly receiving a food reward until condition 3, suggesting that the apparatus was intrinsically reinforcing. Dolphin 4 may have been motivated to solve the apparatus for the challenge itself. Similar results were reported for a sea otter (*Enhydra lutis*) who was able to obtain a food reward but delayed consumption in order to continue interacting with the enrichment device (Hanna, Frick, & Kuczaj, 2016). Contrafreeloading (i.e., choosing to work for food even when food is readily available) is common in a number of species (Menzel, 1991). For example, chimpanzees engaged with a challenge device more often when a non-food reward was available than a food reward (Clark & Smith, 2013). Long-tailed macaques (*Macaca fascicularis*), similarly, spent more time manipulating a puzzle maze than attempting to extract the food (Watson, Shively, & Voytko, 1999). However, Dolphin 4 did not receive a reward when Dolphin 1 or Dolphin 8 were present, marking this as the first report of a dolphin solving a challenging task for an extended period without a tangible reward.

Relinquishing food to a higher-ranking member is a least costly method in terms of energy and risk of aggression when the owner is unlikely to be able to defend the food (Wrangham, 1975). It is unlikely that Dolphin 4 participated with the intent of consuming the food reward since she persisted in solving the apparatus while Dolphin 1 and Dolphin 8 were present. Further, fish may not have been an effective reinforcer for Dolphin 4

21

because she was still regularly nursing and played with the fish before consuming it on the rare occasions that she did obtain the reward.

Dolphin 5 added several weights at the beginning of the study without any food reward. However, in contrast to Dolphin 4, he ceased interacting with the apparatus but continued interacting with the weights for the duration of the study. While Dolphin 4 preferred to solve the apparatus, Dolphin 5 preferred to play with the weights, thus demonstrating individual differences in the reinforcing value of different objects and challenges. The variation in engagement is consistent with previous research on static EED's, in which individual differences in interaction was apparent between individuals (Delfour & Beyer, 2012; Mellen & MacPhee, 2001).

Dolphin 1 and Dolphin 8 sporadically added weights to the apparatus but neither solely solved the apparatus. The food reward provided by the apparatus may not have been valuable enough to warrant consistently retrieving the weights. A food reward of higher magnitude or a higher valued type of fish may have elicited more problem-solving behavior from the adult females. In addition, the study sessions were completed directly after a training session in which they were fed. It is possible that providing the opportunity to solve the apparatus before the training session may have increased motivation to solve the apparatus. However, research with common marmosets (*Callithrix jacchus*) revealed that they spent more time extracting and eating food from a puzzle feeder when they were less hungry (de Rosa, Vitale, & Puopolo, 2003).

Dolphin 4 developed a problem-solving strategy similar to the process modeled by the trainers. Dolphin 4 retrieved one weight at a time and placed it into the apparatus. Contrary to the findings of Kuczaj et al. (2009), Dolphin 4 never added multiple weights simultaneously. Dolphin 4 did not selectively choose the 3-lb weights rather than the 1-lb weights. However, Dolphin 4 did not have an incentive to increase the efficiency of the behavior because she rarely consumed the food reward.

Dolphin 1 and Dolphin 8 did not solve the apparatus as modeled. However, they were still successful in obtaining the food reward by implementing a "sit and wait" strategy that was occasionally followed by non-aggressive displacement. Apart from rarely observed food sharing behavior (Fedorowicz, Beard, & Connor, 2003), highranking dolphins in the dominance hierarchy consume food prior to low-ranking dolphins (Pryor & Shallenberger, 1998). The lack of aggression exhibited after the release of the food reward suggests they were participating in tolerated food theft, as has been reported primates societies (Blurton-Jones, 1987; Feistner & McGrew, 1989).

Conclusion

The dolphins in this study did not carry multiple weights, however, they did develop strategies that were successful in obtaining the food reward. Dolphin 4's continued engagement with the apparatus without receiving a food reward suggests that the challenge of solving the apparatus was intrinsically reinforcing. Thus, individual differences in preference for the types of enrichment (e.g., cognitive challenge, object) and type and magnitude of reward should be assessed. It appeared that the apparatus provided an appropriate level of cognitive challenge and maintained the attention of most of the dolphins. However, the level of effort should be closely monitored, as it may have contributed to the decrease in participation in condition 2. The modifications made in condition 3 increased interest in the apparatus. Therefore, the apparatus may be more

23
engaging when the features of the problem change after fewer trials. Future research should focus on generating other challenging tasks that are intrinsically reinforcing.

CHAPTER II - EFFICACY OF AN INTERACTIVE APPARATUS AS COGNITIVE ENRICHMENT FOR BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) Introduction

Zoos and aquariums often implement environmental enrichment programs to improve the welfare of animals under their care (Harley, Fellner, & Stamper, 2010; Kuczaj et al., 2002). Environmental enrichment involves the addition of stimuli to the environment in order to increase species-specific behavior and provide opportunities for choice and control (Chamove, 1989; White, Houser, Fuller, Taylor, & Elliott, 2003). Environmental enrichment can be achieved through a variety of modalities [see Hoy, Murray, & Tribe (2010) for review], including the addition of objects to the enclosure (e.g., television, balls, and underwater mazes; Clark, Davies, Madigan, Warner, & Kuczaj, 2013; Melfi, 2013; Newberry, 1995; Swaisgood & Shepherdson, 2005; Wells, 2009), novel scents (Fay & Miller, 2015; Samuelson et al., 2017), training (Brando, 2012), and strategic social changes made with the goal of improving welfare (Hill, Guarino, Crandall, Lenhart, & Dietrich, 2015).

The degree of enrichment depends on the audience, as not all environmental enrichment devices (EED's) are equally effective for dolphins (*Tursiops truncatus*) of different ages and sexes (Eskelinen et al., 2015; Neto et al., 2016). Some dolphins exhibit strong preferences for specific objects while showing little interest in others (Delfour & Beyer, 2012; Mellen & MacPhee, 2001). Therefore, the effectiveness of enrichment initiatives should be evaluated to determine the type and quantity necessary to achieve the desired result (Galef, 1999; Mellen & MacPhee, 2001; Morgan, Line, & Markowitz, 1998). Successful cognitive enrichment tasks must: (1) require animals to engage their cognitive skills to solve problems or control the environment and (2) result in positive changes in validated measures of well-being (Clark, 2011).

Indicators of Welfare

Psychological enrichment programs focus on increasing positive indicators of welfare such as increased behavioral diversity, affiliative behaviors, and habitat usage (Kuczaj, Lacinak, & Turner, 1998; Mason, 2010; Swaisgood & Shepherdson, 2005; Wells, 2009) and can result in decreased indicators of negative welfare such as stereotypic and aggressive behaviors (Carlstead, 1998; Waples & Gales, 2002; White et al., 2003). Ethological and physiological studies examining the efficacy of environmental enrichment programs should be conducted to determine the effectiveness of these enrichment devices in creating increased welfare for the animals (Kuczaj et al., 2002).

Behavioral Diversity. Behavioral diversity has been used as a measure of welfare (Galhardo, Appleby, Waran, & dos Santos, 1996), and recent efforts have worked toward validating behavioral diversity as an indicator of welfare using physiological measures (Miller, Pisacane, & Vicino, 2016). Reductions in social behavior and activity levels have been associated with increased cortisol levels, reduced appetite, and illness in dolphins (Waples & Gales, 2002). Changes in behavioral diversity and activity levels can be used as an early detection system for identifying environmental and physiological stressors.

Social Cohesion. Wild dolphins have dynamic social lives in fission-fusion societies, where they learn to employ a wide variety of foraging strategies (Duffy-Echevarria, Connor, & St. Aubin, 2008; Similä & Ugarte, 1993; Smolker, Richards, Connor, Mann, & Berggren, 1997). The plethora of socially learned foraging strategies and synchronous behaviors (Connor, Smolker, & Bejder, 2006; Fellner, Bauer, Stamper, Losch, & Dahood, 2013) exhibited by wild dolphins suggests that some of their daily problems can be addressed by cooperating, which aids in social cohesion. Similarly, cooperative play is particularly important in acquiring information about conspecifics and developing social skills (Kuczaj & Eskelinen, 2014). Affiliative behaviors such as social play, rubbing, and synchronous swimming have been considered variables indicative of positive welfare, leading to health benefits (Clark et al., 2013; Held & Spinka, 2011; Hill, Dietrich, et al., 2015; Hill, Guarino, et al., 2015; Kuczaj et al., 2006).

Another important aspect of enrichment may be its availability to all the members of the social group. For example, dominant animals often co-opt access to single user apparatuses, thereby preventing access to subordinate individuals (Reamer et al., 2014; Wergård, Westlund, Spångberg, Fredlund, & Forkman, 2016). Whereas non-interactive EED's dolphins (e.g., buoys, balls, or floating mats) are engaging on the individual level, interactive apparatuses that allow multiple animals to participate simultaneously may encourage social behaviors and cooperation.

Habitat Usage. Habitat utilization has been used an indicator of welfare when assessing the efficacy of enrichment. For example, food hiding programs in the enclosures of land animals (Charmoy, Sullivan, & Miller, 2015), and the introduction of novel scents to sea lions (Samuelson et al., 2017) have successfully increased habitat usage. Dolphins in human care spend more time at the surface of the water than their wild counterparts (Galhardo et al., 1996). However, exploration of their full habitat can be promoted by providing submerged EEDs. Dolphins spend significantly more time underwater when submerged enrichment is present (Clark et al., 2013).

27

Challenging Enrichment Devices

Research on enrichment devices has mainly focused on non-interactive objects (Clark et al., 2013; Delfour & Beyer, 2012). Although some unresponsive objects are effective in increasing species-specific behavior and decreasing stereotypic behavior (Delfour & Beyer, 2012; Hunter, Bay, Martin, & Hatfield, 2002; Smith & Litchfield, 2010), providing cognitively challenging enrichment may achieve longer lasting benefits and expand overall knowledge of dolphin cognition (Harley et al., 2010; Meehan & Mench, 2007). Cognitive challenges have benefitted the well-being of farm animals (Langbein, Siebert, & Nürnberg, 2009; Puppe, Ernst, Schon, & Manteuffel, 2007) and are considered a potential form of enrichment for dolphins (Clark, 2011; Clark, 2013). In order to assess if problem-solving apparatuses were appropriately challenging and enriching to dolphins, Clark and colleagues created a two-dimensional underwater maze device (Clark et al., 2013). They found that dolphins who interacted with the maze used a variety of problem-solving strategies and spent more time engaging in play behaviors while the apparatus was being presented.

Knowledge regarding dolphins' ability to process and respond to stimuli can aid in the creation of well-informed animal management and conservation programs based on scientifically valid species-specific data (Ross, 2010). One program utilizing cognitive research at Disney's The Seas resulted in positive effects to the dolphins' in their care (Harley et al., 2010). Although the enrichment value of each type of task was not directly measured, this program provided a substantial amount of scientific data about dolphin's perceptual systems and cognitive processing, while potentially enriching the lives of the subjects. Furthermore, the results of this program have been used to guide the studies of wild dolphins (e.g., Connor et al., 2006; Gotz, Verfuss, & Schnitzler, 2006; Janik, 2000). *Choice and Control*

Research suggests that allowing animals to choose or have control over some aspect of their environment leads to enhanced well-being (Bassett & Buchanan-Smith, 2007; Griffith, Pryke, & Buttemer, 2011; Sambrook & Buchanan-Smith, 1997). For example chimpanzees, gorillas, and polar bears exhibited more species-specific behaviors and more social behaviors when given the choice of indoor and outdoor enclosures (Kurtycz, Wagner, & Ross, 2014; Ross, 2006). Dolphins' interactions with trainers and guests have been found to be enriching and give them control within their environment (Miller et al., 2013). Voluntary participation in challenging, species-appropriate enrichment allows animals to have active control over their environment (Clark, 2011; Laule & Desmond, 1998; Manteuffel, Langbein, & Puppe, 2009).

Habituation

Non-interactive EED's can easily become standard to the environment and no longer elicit positive effects (Delfour & Beyer, 2012). Habituation can be prevented in several ways. Devices that can be controlled or manipulated by the animal are more resistant to habituation (Markowitz & Line, 1989). Presenting objects, even noninteractive ones, on a variable schedule maintains their enriching quality for a longer period of time (Kuczaj et al., 2002). Devices that provide edible, tangible, or social reinforcement, especially when the reinforcement is difficult to obtain, produce stronger and longer lasting enriching effects (Neto et al., 2016; Tarou & Bashaw, 2007). The enriching effects of interactive tasks can also be maintained when the food reinforcement delivered is different from food delivered during regular feedings (Murphy, Mcsweeney,

29

& Kowal, 2003). Presenting problem-solving opportunities combines these tactics because the device can be manipulated, supply variable extrinsic reinforcement, and be presented on a variable schedule, resulting in the devices that could be enriching for extended periods of time.

Purpose of Study

The purpose of the present study was to determine if a submerged problemsolving apparatus is enriching to dolphins by assessing indicators of positive welfare, social cohesion, and habitat usage. The following research questions will be examined: (1) Does the presentation of a problem-solving task enhance welfare and increase habitat usage?; (2) If so, how long do the benefits persist after the task is no longer presented? It was hypothesized that indicators of positive welfare, social cohesion, and habitat usage would increase and that indicators of positive welfare and social cohesion would persist, though habitat usage may return to baseline.

Methods

Eight Atlantic bottlenose dolphins (*Tursiops truncatus*), housed at the Brookfield Zoo in Brookfield, Illinois, USA were observed to examine the enrichment efficacy of a submerged interactive apparatus over a 10-month period. The pod consisted of one female/male mother-calf dyad, one female/female mother-calf dyad, three sub-adult females, and one male calf (Table 4). The enclosure consisted of four interconnected pools: an oblong front pool (33.5 m across, 12.2 m wide, and 6.7 m deep), two circular rear pools (10.7 m diameter, 4.3 m deep), and a medical pool (7.6 m diameter, 2.4 m deep; Figure 6). Dolphins received their normal non-interactive daily enrichment (e.g., balls, buoys, water hoses, hula hoops, etc.) throughout the present study.

Table 4

Demographic information on participants

Dolphin	Age	Group	Sex
Dolphin 1	30	2	Female
Dolphin 2	11	1	Female
Dolphin 3	2	2	Male
Dolphin 4	1	1	Female
Dolphin 5	2	2	Male
Dolphin 6	13	1	Female
Dolphin 7	14	1	Female
Dolphin 8	34	2	Female





Data were collected for eight weeks prior to the introduction of an interactive enrichment apparatus, during the presentation of the apparatus (18 weeks; see Chapter I for the protocol), and for eight weeks after the apparatus was no longer presented. Realtime observations were conducted from underwater viewing windows and recorded using Animal Behaviour Pro (2012). Continuous sampling of behavior events (e.g., interaction with conspecifics, objects, and trainers/guests) and instantaneous sampling of swim state and location were recorded. Swim states and locations are operationally defined in Appendix A and Appendix B, respectively. Operational definitions for behavior events are listed in Appendix C and categorized in Appendix D. Operational definitions are adapted, in part, from Dudzinski (1996), Harvey (2015), and Hill et al. (2015). Observations were collected on a randomized, counterbalanced schedule five days a week between the hours of 0630-1800. Data were not collected during shows, training sessions, or during trials with the apparatus.

A total of 18 hours of behavioral observations were recorded each week (Quirke & O'Riordan, 2012). Behavioral data were gathered following a protocol of subsequent 15-minute focal follows for each dolphin. Instantaneous sampling was used to record the swim state and location of the focal dolphin every one minute. Continuous sampling was used to record all other behaviors. A single observer collected all data via direct observation.

Inter-observer agreement (IOA) was evaluated for 16 observation periods (2 pretreatment and 2 post-treatment observations per animal). IOA was achieved across subjects, with both coders reaching at least 80% reliability (Haidet, Tate, Divirgilio-Thomas, Kolanowski, & Happ, 2009). A Pearson's correlation coefficient was calculated to measure pairwise correlations among raters (Burghardt et al., 2012). There was a strong positive correlation on the continuous data (r = .944) and good agreement on instantaneous data ($\kappa = 0.605$, p < 0.001) for the pre-treatment observations and strong positive correlation on the continuous data (r = .950) and very good agreement on instantaneous data ($\kappa = 0.872$, p < 0.001) for the post-treatment observations. To ensure intra-coder reliability throughout the study, three 1-hour videos were scored before beginning of pre-treatment phase, treatment phase, and post-treatment phase. There was a strong positive correlation on the continuous data between pre-treatment and treatment phases (r = .947) and between treatment and post-treatment phases (r = .946). There was a very good agreement on the instantaneous data between pre-treatment and treatment phases ($\kappa = 0.884$, p < 0.001) and between treatment and post-treatment phases ($\kappa =$ 0.933, p < 0.001).

Due to the small sample size, all analyses were conducted using non-parametric tests and differences were considered significant at p < 0.05. Data were analyzed using R and SPSS. To examine differences in location and swim state using the one-minute samples, the total number of occurrences in each category was summed and divided by the total number of visible scans for each dolphin per session. The session data were averaged for each dolphin per week and phase, to create an average amount of time spent in a specific location and swim state. To determine the significant changes in location and swim state in response to the apparatus between time periods, the Shannon-Weiner diversity index (Peet, 1974) was calculated, as it has the ability to identify subtle changes in behavioral diversity (DeJong, 1975; Shannon & Weaver, 1949). Non-species-specific behaviors were not included in the behavioral diversity analyses. Behavioral diversity is notated H values, with higher H-values indicating a greater number of behaviors and/or an even distribution of behaviors (Peet, 1974). The Shannon index (H) is calculated as

$$H = -\sum_{i=1}^{R} p_i \ln(\mathbf{p}_i)$$

-

where p_i is the proportion of the behavior category. An absence of behaviors listed in the ethogram resulted in a diversity index of zero. Differences in diversity indices were compared between pre-treatment, treatment, and post-treatment phases using a Freidman's test. In the case of overall significance (p < 0.005), a Wilcoxon Signed Ranks test was calculated.

To assess differences in behavior categories using the continuous samples, the total number of events in each category (i.e., social active, social agonistic, social sexual, solitary active, solitary sexual, and solitary stereotypical) was summed and divided by the total number of minutes visible. The session data was averaged for each dolphin per week and per phase. To determine the significant changes in behavior in response to the apparatus between phases, the Shannon-Weiner diversity index was used (Peet, 1974). A Friedman's test was used to test significant differences in behaviors between the three phases. In the case of overall significance (p < 0.005), a Wilcoxon Signed Ranks test was calculated. Differences in overall diversity indices were compared between pre-treatment, treatment, and post-treatment phases using a Freidman's test.

Results

Behavior Data

There was a marginal effect of phase for diversity of behavior, ($\chi^2(2) = 5.250$, p = 0.079; Figure 7). Post hoc comparisons were significant between the treatment and post-treatment phase (Z = -2.100, p = 0.039, r = -0.53). Post hoc comparisons were not significant between the pre-treatment and treatment phases (Z = -1.680, p = 0.109, r = 0.42) and the pre-treatment and post-treatment phases (Z = -1.400, p = 0.195, r = -0.35). The highest indices were found in the treatment phase and the lowest indices were found

in the post-treatment phase. The highest mean diversity index values occurred in the treatment phase for Dolphin 1, Dolphin 3, Dolphin 4, Dolphin 5, Dolphin 6, and Dolphin 8. Shannon-Weiner index values for each phase by dolphin are presented in Figure 8. Mean diversity indices for all individuals for each phase are given in Table 5. Shannon-Weiner index values for each week are given in Figure 9.

Dolphins predominantly engaged in social active (group average = 48.9% of observed behaviors) and solitary active (group average = 36.2% of observed behaviors) behaviors in all conditions. There were statistically significant differences for social active behaviors between phases ($\chi^2(2) = 9.750$, p = 0.005). Post hoc tests were significant between the pre-treatment and post-treatment phases (Z = -2.521, p = 0.012, r = -0.63) and the treatment and post-treatment phases (Z = -2.240, p = 0.025, r = -0.56). The post hoc test was not significant between the pre-treatment and treatment phases (Z =-0.980, p = 0.327, r = -0.25). There were statistically significant differences for social sexual behaviors between phases ($\chi^2(2) = 7.750$, p = 0.018). Post hoc tests were significant between the treatment and post-treatment phases (Z = -2.380, p = 0.017, r = -0.59). The post hoc test was not significant between the pre-treatment and treatment phases (Z = -1.820, p = 0.069, r = -0.46) and the pre-treatment and post-treatment phases (Z = -1.820, p = 0.069, r = -0.46). There were statistically significant differences for solitary active behaviors between phases ($\chi^2(2) = 12.250$, p = 0.001). The post hoc test was significant between the pre-treatment and post-treatment phases (Z = -2.521, p =0.012, r = -0.63). The post hoc tests were not significant between the pre-treatment and treatment phases (Z = -1.960, p = 0.050, r = -0.49) and the treatment and post-treatment phases (Z = -1.960, p = 0.050, r = -0.49). There were no statistically significant

differences for the social agonistic ($\chi^2(2) = 3.250$, p = .236), solitary sexual ($\chi^2(2) = 2.00$, p = 1.000), and solitary stereotypical ($\chi^2(2) = 5.250$, p = 0.79) behavior categories between phases.



Overall Behavioral Diversity

Figure 7. Shannon-Weiner index values for behavioral diversity.

Behavioral Diversity



Figure 8. Shannon-Weiner index values for each individual by phase.

The pre-treatment phase is denoted with a 0, the treatment phase is denoted with a 1, and the post-treatment phase is denoted with a 2.

Table 5

Mean Phase Behavioral Diversity Indices

Dolphin	Pre-treatment	Treatment	Post-treatment
Dolphin 1	0.681	0.764	0.706
Dolphin 2	0.702	0.625	0.687
Dolphin 3	0.832	0.880	0.740
Dolphin 4	0.700	0.839	0.578
Dolphin 5	0.555	0.691	0.573
Dolphin 6	0.640	0.719	0.576
Dolphin 7	0.710	0.674	0.609
Dolphin 8	0.673	0.705	0.683
Average	0.687	0.737	0.644

Weekly Behavioral Diversity



Figure 9. Shannon-Weiner index values for behavioral diversity by week. *Swim State and Habitat Usage*

Diversity of swim states did not differ significantly between pre-treatment, treatment, and post-treatment phases ($\chi^2(2) = 0.250$, p = 0.967), with the highest indices found in the post-treatment phase. Mean swim state diversity indices for all individuals for each phase are given in Table 6. Diversity of locations differed significantly ($\chi^2(2) =$ 7.000, p = 0.030), with the highest indices found in the post-treatment phase. The post hoc test was significant between the treatment and post-treatment phases (Z = -2.380, p =0.016, r = -0.60). The post hoc tests were not significant between the pre-treatment and treatment phases (Z = -0.420, p = 0.742, r = -0.11) and the pre-treatment and posttreatment phases (Z = -1.960, p = 0.055, r = -0.49). Mean location diversity indices for all individuals for each phase are given in Table 7. Mean proportion of time in each swim state is illustrated in Figure 5. There were statistically significant differences in swim state ($\chi^2(2) = 6.000, p = 0.028$). However, the post hoc test was not significant (Z = -1.604, p = 0.109, r = -0.40). There were no statistically significant differences in location ($\chi^2(2) = 4.667, p = 0.194$). The proportion of time spent in social swim states was highest in the treatment phase at 57.8% and was lowest in the pre-treatment phase at 50.8%. Mean proportion of time in each location is illustrated in Figure 6. The proportion of time spent in the bottom of the habitat highest in the treatment phase at 38.9%. They spent 32.6% of their time at the bottom in the pre-treatment phase and 29.5% in the post-treatment phase.

Table 6

Mean	Phase	Swim	State	Diversity	Indices
11100000	1 110050	511111	Siene	Direibily	manees

Dolphin	Pre-treatment	Treatment	Post-treatment
Dolphin 1	0.729	0.718	0.733
Dolphin 2	0.613	0.743	0.839
Dolphin 3	0.724	0.715	0.767
Dolphin 4	0.648	0.709	0.672
Dolphin 5	0.711	0.581	0.660
Dolphin 6	0.708	0.841	0.880
Dolphin 7	0.758	0.840	0.772
Dolphin 8	0.793	0.653	0.788
Average	0.711	0.725	0.764

Table 7

Dolphin	Pre-treatment	Treatment	Post-treatment
Dolphin 1	0.951	0.988	1.022
Dolphin 2	0.885	0.898	1.044
Dolphin 3	0.985	0.992	1.031
Dolphin 4	0.996	1.019	1.016
Dolphin 5	1.043	0.929	1.005
Dolphin 6	0.875	0.876	1.055
Dolphin 7	1.032	0.947	1.058
Dolphin 8	1.033	0.920	1.036
Average	0.975	0.946	1.034

Mean Phase Location Diversity Indices



Figure 10. Mean proportion of time spent in a given swim state



Figure 11. Mean proportion of time spent in a given location

Discussion

There were no significant differences in behavioral diversity indices between the pre-treatment, treatment, and post-treatment phases. However, there was a large effect size between the treatment and post-treatment phases and a medium effect size between the pretreatment and treatment phases. Given this study's small sample size, it is likely that omnibus statistical tests were underpowered; nonetheless, the presence of medium to large effect sizes for post hoc comparisons suggests that the interactive apparatus may have been impactful with respect to behavioral diversity. Furthermore, the behavioral diversity indices were highest when dolphins had access to the interactive apparatus. Differences in swim states and locations were non-significant, however, social swim states and usage of the bottom of the habitat were highest during the treatment phase.

Combined, this suggests that the interactive apparatus may have resulted small changes in behavior.

Environmental enrichment is a crucial component of improving the welfare of marine mammals (Shepherdson et al., 1998; Swaisgood et al., 2001). Individual differences in the amount and type of interaction with EEDs illustrates the importance of assessing the efficacy of enrichment categories and implementation protocols (Delfour & Beyer, 2012). Variation in preferences for different types of enrichment and certain types of challenges is apparent in response to enrichment (Clark & Smith, 2013). Assessing behavioral diversity, social cohesion, and habitat usage is necessary when developing environmental enrichment of this nature.

Enriching interactive apparatuses require that the apparatus be an appropriate cognitive challenge and provide tangible or intrinsic reinforcement. While some frustration is necessary when problem-solving, an inappropriate challenge may result in an increase in undesired self-injurious or stereotypical behaviors (Clark & Smith, 2013; Leavens, Aureli, Hopkins, & Hyatt, 2001). Non-intrinsically enriching devices must deliver a reward that is of high enough value for unsolicited participation to occur (de Rosa et al., 2003). However, if used in social situations, the reward should be high enough value that it warrants participation or the attention of individuals who don't find the apparatus alone enriching but caution should be taken so that the high-value reward does not illicit aggressive competitive behaviors.

The interactive apparatus presented in the present study may have resulted in small, but measurable changes in behavior. The dolphins regularly solved the apparatus throughout the treatment phase. It also provided a reward that retained the interest of the participants who did not actively try to solve the apparatus. Habituation to non-interactive EEDs occurs rather quickly (Kuczaj et al., 2002). The results in the present study are consistent with previous research in which a challenging maze device was resistant to habituation (Clark et al., 2013).

Increasing habitat usage is one of the goals of environmental enrichment. The highest proportion of time spent in the bottom of the habitat occurred during the treatment. The sinking weights used with the apparatus required the dolphins to navigate the entire depth of their habitat in order to participate, which may have altered their exploratory behaviors. An increase in exploration behaviors has been previously suggested as benefit of cognitive challenges because animals seek out novel problemsolving situations. Furthermore, this is consistent with Clark et al.'s (2013) investigation of an underwater maze device, in which dolphins spent more time at the same pool depth as the device and interacted more with other underwater non-interactive EED's.

Although there was no distinctive indication that the dolphins cooperated to solve the apparatus, the rates of social behaviors and social swim states were highest during the treatment phase. Synchronicity in dolphins can be indicative of strong social bonds or as an indicator of stress/threat defense (Connor et al., 2006). The improved synchronicity is most likely a result of an increase in social cohesion, as additional indications of stress, such as inactivity and social isolation (Waples & Gales, 2002), were lowest in the treatment phase.

Dolphin 2's behavior proved to be the most difficult to interpret. Her behavioral diversity indices were lowest during the treatment phase due to a less even distribution of social active and solitary active behaviors. However, the rate of stereotypical behaviors

was lowest during the treatment phase, suggesting that she did not find the apparatus aversive. The author hypothesizes that highest behavior diversity indices were related to the rate of social behaviors. As Dolphin 2 was the recipient of the highest number of agonistic behaviors, the rate of social behaviors may have resulted in interactions that caused her to switch from social to solitary more often.

Welfare can be improved by allowing the animal to have control over its environment (Bassett & Buchanan-Smith, 2007). Dolphins had the choice to interact with the apparatus and control over it because they could add weights and monitor progress. Dolphin 4 and Dolphin 5 provide an example of the benefits of allowing animals to choose their level of interaction with enrichment. They interacted in very different ways with the apparatus. Dolphin 4 regularly solved trials while Dolphin 5 carried the weights and watched Dolphin 4 solve the trials (see Chapter I for details). However, they had the largest differences in diversity indices between the treatment phase and other phases. *Limitations*

While it appears that the apparatus was enriching, the presence of the researcher and assisting trainer or the additional time attending to the trainer during the trials may have also altered their behavior. Human interaction is enriching even when no objects are present (Eskelinen et al., 2015). Trials took place during a 1-hour period in which humandolphin interactions did not normally take place. Thus, the increased activity and human interaction could have provided additional enrichment.

Conclusion

The results indicate that the interactive apparatus may have produced small but measurable changes in behavior. There was a marginal effect of phase for diversity of behavior, with the highest behavioral diversity indices found in the treatment phase. In addition, social swim states and usage of the bottom of the habitat were highest during the treatment phase, suggesting that it may have provided benefits beyond non-interactive enrichment. Further, the study highlights the different ways in which individuals may have been affected by EEDs. Some may have benefitted from the apparatus in certain aspects, while others remained unaffected. Future research should focus individual differences in participation on different levels and types of cognitively challenging tasks.

Swim State	Category	Definition
Solitary Swim	Solitary	Dolphin swims independently, not synchronous with any conspecific
Solitary Surface Resting	Solitary	Dolphin remains stationary at the surface of the water column independently
Solitary Bottom Resting	Solitary	Dolphin remains stationary at the bottom of the water column independently
Solitary Vertical Resting	Solitary	Dolphin remains stationary while positioned vertically in the water column
Solitary Wall Swim	Solitary	Dolphin swims with a pectoral fin and/or dorsal fin against the pool wall, using it as a guide
Group Swim	Social	Three or more dolphins (not including a mother/calf dyad) swimming synchronously within one dolphin-body-length (approx. 2.5 m)
Group Swim with Calf	Social	Three or more dolphins including a mother/calf dyad swimming synchronously within one dolphin-body-length (approx. 2.5 m)
Group Surface Resting	Social	Three or more dolphins remain stationary at the surface of the water column within one dolphin-body-length (approx. 2.5 m)
Group Bottom Resting	Social	Three or more dolphins remain stationary at the bottom of the water column within one dolphin-body-length (approx. 2.5 m)
Mother-Calf Swim	Social	Mother/calf dyad swimming synchronously within one dolphin- body-length (approx. 2.5 m)
Group Social Swim	Social	Three or more dolphins interacting non-synchronously within one dolphin-body-length (approx. 2.5 m; e.g., play)
Pair Social Swim	Social	Two dolphins interacting non-synchronously within one dolphin- body-length (approx. 2.5 m; e.g., play)
Pair Swim	Social	Two dolphins (not a mother/calf dyad) swimming synchronously within one dolphin-body-length (approx. 2.5 m)
Pair Surface Resting	Social	Two dolphins remain stationary at the surface of the water column within one dolphin-body-length (approx. 2.5 m)
Pair Bottom Resting	Social	Two dolphins remain stationary at the bottom of the water column within one dolphin-body-length (approx. 2.5 m)
Out of Sight	N/A	Dolphin is out of view

APPENDIX A – Swim State Operational Definitions

APPENDIX B – Location Operational Definitions

Location	Definition
Main Pool, Top	Dolphin is located in the top 1/3 of the water column in the main pool
Main Pool, Middle	Dolphin is located in the middle 1/3 of the water column in the main pool
Main Pool, Bottom	Dolphin is located in the bottom 1/3 of the water column in the main pool
North Pool, Top	Dolphin is located in the top 1/3 of the water column in the north pool
North Pool, Middle	Dolphin is located in the middle 1/3 of the water column in the north pool
North Pool, Bottom	Dolphin is located in the bottom 1/3 of the water column in the north pool
South Pool, Top	Dolphin is located in the top 1/3 of the water column in the south pool
South Pool, Middle	Dolphin is located in the middle 1/3 of the water column in the south pool
South Pool, Bottom	Dolphin is located in the bottom $1/3$ of the water column in the south pool
Medical Pool	Dolphin is located in the medical pool

Behavior	Category(s)	Type(s)	Definition
Beach	Solitary	Active	Dolphin slides more than one-third of its body onto the slide out
Bite/Rake	Social	Agonistic	Dolphin forcefully rubs its teeth or closes mouth around another dolphin
Bite/Rake Recipient	Social	Agonistic	Another dolphin rubs its teeth or closes its mouth with force around the focal dolphin
Bow	Solitary	Active	Dolphin fully jumps out of the water and re-enters the water head first
Breach	Solitary	Active	Dolphin fully jumps out of the water and re-enters the water on its lateral side
Bubble Burst	Solitary	Active	Dolphin produces large bubble/bubbles from the blowhole similar to those produced by scuba equipment
Bubble Ring	Solitary	Active	Dolphin produces bubbles in the shape of a ring from the blowhole
Bubble Trail	Solitary	Active	Dolphin produces a series of small bubbles from the blowhole that form a trail
Chase	Social	Active	Rapid and persistent pursuit of another dolphin
Erection	Social/ Solitary	Sexual	Dolphin's penis is visible
Flee	Social	Active	Abrupt, rapid, and immediate departure in response to the actions of another dolphin
Fluke Slap	Solitary	Active	Dolphin slaps the surface of the water with its flukes in a quick manner
Fluke Splash	Solitary	Active	Dolphin swims ventral side up near the surface of the water and splashes water upward with their flukes
Genital Rub	Social	Sexual	Dolphin rubs the genital area of another dolphin with any part of their body other than their rostrum or genitals
Genital Rub Recipient	Social	Sexual	Another dolphin rubs the genital area of the focal dolphin with any part of their body other than their rostrum or genitals
Goosing/ Push-Up	Social	Sexual	Dolphin inspects or contacts the genital area of another dolphin with their rostrum
Goosing/ Push-Up Recipient	Social	Sexual	Another dolphin inspects or contacts the genital area of the focal dolphin with their rostrum
Group Social Ball	Social	Sexual	Three or more dolphins rapidly swim around each other and appear to be "wrestling"

APPENDIX C – Behavior Event Operation Definitions

Head Jerk	Social	Agonistic	Dolphin abruptly movies their head vertically or horizontally
Head Jerk Recipient	Social	Agonistic	Another dolphin abruptly movies their head vertically or horizontally in the direction of the focal dolphin
Herd	Social	Agonistic	Dolphin is directing another dolphin's movements from behind
Herd Recipient	Social	Agonistic	Another dolphin is directing the focal dolphin's movements from behind
Hit	Social	Active	Dolphin contacts another dolphin using their rostrum or fluke in a quick manner
Hit Recipient	Social	Active	Another dolphin contacts the focal dolphin with their rostrum or fluke in a quick manner
Interact With Object	Solitary	Active	Dolphin independently interacts with an object
Interact With Pool Object	Solitary	Active	Dolphin independently interacts with a part of the pool (e.g., gate or outflow pipe)
Interact With Trainer	Solitary	Active	Dolphin independently interacts with or visually inspects a trainer
Interact With Bubble	Solitary	Active	Dolphin independently interacts with bubbles or moving water
Interact With Research- er	Solitary	Active	Dolphin independently visually inspects a researcher at an underwater viewing window
Interact With Guest	Solitary	Active	Dolphin independently visually inspects or interacts with guest at an underwater viewing window
Jaw Pop	Social	Agonistic	Dolphin produces a loud popping sound coupled with a fast open and close of the mouth
Jaw Pop Recipient	Social	Agonistic	Another dolphin produces a loud popping sound coupled with a fast open and close of the mouth in the direction of the focal dolphin
Mount Pool	Solitary	Sexual	Dolphin mounts a pool wall, window or floor
Mounting	Social	Sexual	Dolphin mounts another dolphin by orienting its genital region to another dolphin's genital region or a dolphin inserts another dolphin's dorsal fin in their genital slit
Mounting Recipient	Social	Sexual	Another dolphin mounts the focal dolphin by orienting its genital region to the focal dolphin's genital region or another dolphin inserts the focal dolphin's dorsal fin in their genital slit

Mouthing	Social	Active	Dolphin has mouth around a conspecific's body, or around an object, but is not biting down
Mouthing Recipient	Social	Active	Focal dolphin has another dolphin's mouth around its body but the dolphin is not biting down
Nursing	Social	Active	Calf in position near mammary slits with rostrum near/in slits
Open Mouth	Social	Active	Dolphin separates its jaws to expose teeth
Open Mouth Recipient	Social	Active	Dolphin is the recipient of another dolphin that separates its jaws to expose teeth
Other	Social/ Solitary	Any	Any behavior not listed in the ethogram
Petting	Social	Active	Pectoral fin to pectoral fin rubbing where active movement is observed
Porpoise	Solitary	Active	Dolphin jumps partially out of the water (flukes remain in water) and re-enters the water head first
Regurg- itation	Solitary	Stereotypical	Dolphin casts up previously ingested food
Re- ingestion	Solitary	Stereotypical	Re-ingestion of regurgitated food
Social Interact With Object	Social	Active	Two or more dolphins simultaneously interact with an object
Social Interact With Pool Object	Social	Active	Two or more dolphins simultaneously interact with a part of the pool (e.g., gate or outflow pipe)
Social Interact With Trainer	Social	Active	Two or more dolphins simultaneously interact with or visually inspects a trainer
Social Interact With Bubble	Social	Active	Two or more dolphins simultaneously interact with bubbles or water
Social Interact With Research- er	Social	Active	Two or more dolphins simultaneously participate in close visual inspection of a researcher at an underwater viewing window
Social Interact With Guest	Social	Active	Two or more dolphins simultaneously participate in close visual inspection or interact with guest at an underwater viewing window

Spy Hop	Solitary	Active	Dolphin raises and lowers half of its body out of the water in a vertical position
Tactile/ Rub	Social	Active	Dolphin contacts or actively rubs another dolphin a manner that is not considered sexual contact
Tactile/ Rub Recipient	Social	Active	Another dolphin contacts or actively rubs the focal dolphin a manner that is not considered sexual contact
Tactile/ Rub Pool	Solitary	Active	Dolphin contacts or actively rubs any part of their body on the pool wall
Tongue	Solitary	Active	Dolphin manipulates their own tongue or sticks it out of their mouth
Ventral Swim	Solitary	Active	Dolphin swims ventral side up for more than 3 seconds

Category	Orientation	Туре	Behavior
Social Behaviors	Dolphin	Active	Chase, Flee, Hit, Hit Recipient, Mouthing, Mouthing Recipient, Nursing, Open Mouth, Open Mouth Recipient, Petting, Tactile/Rub, Tactile/Rub Recipient
		Agonistic	Bite/Rake, Bite/Rake Recipient, Head Jerk, Head Jerk Recipient, Herd, Heard Recipient, Jaw Pop, Jaw Pop Recipient
		Sexual	Erection, Genital Rub, Genital Rub Recipient, Goosing/Push-Up, Goosing/Push-Up Recipient, Group Social Ball, Mounting, Mounting Recipient
	Human	Active	Social Interact With Trainer, Social Interact With Researcher, Social Interact With Guest
	Object	Active	Social Interact With Object, Social Interact With Bubble, Social Interact With Pool Object
	Other		Any social behavior not listed
Solitary Behaviors	None	Active	Beach, Bow, Breach, Bubble Burst, Bubble Ring, Bubble Trail, Fluke Slap, Fluke Splash, Porpoise, Spy Hop, Tongue, Ventral Swim
	None	Stereotypical	Regurgitation, Re-ingestion
	Human	Active	Interact With Trainer, Interact With Researcher, Interact With Guest
	Object	Sexual	Mount Pool, Solo Erection
	Object	Active	Interact With Bubble, Interact With Object, Interact With Pool Object
	Other		Any independent behavior not listed

APPENDIX D – Behavior Categories

APPENDIX E – IACUC Approval Letter



INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

118 College Drive #5116 | Hattiesburg, MS 39406-0001 Phone: 601.266.6791 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:

16052607

PROJECT TITLE:

PROPOSED PROJECT DATES: PROJECT TYPE: PRINCIPAL INVESTIGATOR(S): DEPARTMENT: FUNDING AGENCY/ SPONSOR: N/A IACUC COMMITTEE ACTION: PROTOCOL EXPIRATON DATE: September 30, 2018

Efficacy of cognitive enrichment for bottlenose dolphins (Tursiops truncatus): Evaluation of planning abilities through the use of a novel problem -solving task 05/2016 - 09/2018 New Don Sacco Psychology Full Committee Approval

Date

Frank Moore, PhD IACUC Chair

05/26/16

REFERENCES

- Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology*, 18, 1415–1419.
- Barth, J., Povinelli, D. J., & Cant, J. G. H. (2004). Bodily Origins of Self. In D. Beike, J. Lampinen, & D. Behrend (Eds.), *The Self and Memory* (pp. 11–44). New York, NY: Psychology Press.
- Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, 102, 223–245.
- Blurton-Jones, N. G. (1987). Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Biology and Social Life*, *26*(1), 31–54.
- Bourjade, M., Call, J., Pelé, M., Maumy, M., & Dufour, V. (2014). Bonobos and orangutans, but not chimpanzees, flexibly plan for the future in a token-exchange task. *Animal Cognition*, 17(6), 1329–1340.
- Brando, S. I. C. A. (2012). Animal learning and training: implications for animal welfare.*The Veterinary Clinics of North America. Exotic Animal Practice*, 15, 387–398.
- Burghardt, G. M. (2005). *The Genesis of Animal Play: Testing the Limits*. Boston, MA: MIT Press.
- Burghardt, G. M., Bartmess-Levasseur, J. N., Browning, S. A., Morrison, K. E., Stec, C.
 L., Zachau, C. E., & Freeberg, T. M. (2012). Minimizing Observer Bias in
 Behavioral Studies: A Review and Recommendations. *Ethology*, *118*, 511–517.
- Carlstead, K. (1998). Determining the causes of stereotypic behavior in zoo carnivores:Toward appropriate enrichment strategies. In D. J. Shepherdson, J. Mellen, & M.Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals*

(pp. 172–183). Washington DC: Smithsonian Institution Press.

- Chamove, A. S. (1989). Environmental enrichment: a review. *Animal Technology*, 40(3), 155–178.
- Charmoy, K., Sullivan, T., & Miller, L. J. (2015). Impact of Different Forms of Environmental Enrichment on Foraging and Activity Levels in Gorillas (Gorilla gorilla gorilla). *Animal Behavior and Cognition*, 2(3), 233–240.
- Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*, 1–12.
- 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*, 1–6.
- Clark, F. E., Davies, S. L., Madigan, A. W., Warner, A. J., & Kuczaj, S. A. I. (2013).
 Cognitive enrichment for bottlenose Dolphins (Tursiops truncatus): Evaluation of a novel underwater maze device. *Zoo Biology*, *32*(6), 608–619.
- Clark, F. E., & Smith, L. J. (2013). Effect of a cognitive challenge device containing food and non-food rewards on chimpanzee well-being. *American Journal of Primatology*, 75(8), 807–816.
- Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, Tursiops aduncus. *Animal Behaviour*, 72(6), 1371–1378.
- 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 (Ed.), *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago, IL: University of

Chicago Press.

- D'Mello, S., & Franklin, S. (2011). A cognitive model's view of animal cognition. *Current Zoology*, *57*(4), 499–513.
- de Rosa, C., Vitale, A., & Puopolo, M. (2003). The puzzle-feeder as feeding enrichment for common marmosets (Callithrix jacchus): a pilot study. *Laboratory Animals*, 37, 100–107.
- DeJong, T. M. (1975). A comparison of three diversity indices based on their components of richness and evenness. *Oikos*, 222–227.
- Delfour, F., & Beyer, H. (2012). Assessing the effectiveness of environmental enrichment in bottlenose dolphins (Tursiops truncatus). *Zoo Biology*, 31, 137– 150.
- Dudzinski, K. M. (1996). Communication and behavior in the Atlantic spotted dolphins (Stenella Frontalis): Relationships between vocal and behavioral activities.
- 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(1), 202–206.
- Dufour, V., & Sterck, E. H. M. (2008). Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. *Behavioural Processes*, *79*, 19–27.
- Eskelinen, H. C., Winship, K. A., & Borger-turner, J. L. (2015). Sex, Age, and Individual
 Differences in Bottlenose Dolphins (Tursiops truncatus) in Response to
 Environmental Enrichment. *Animal Behavior and Cognition*, 2(3), 241–253.
- Fay, C., & Miller, L. J. (2015). Utilizing Scents as Environmental Enrichment :Preference Assessment and Application with Rothschild Giraffe. *Animal Behavior*

and Cognition, 2(3), 285–291.

- Fedorowicz, S. M., Beard, D. A., & Connor, R. C. (2003). Food sharing in wild bottlenose dolphins. (Tursiops truncatus). *Aquatic Mammals*, 29(3), 355–359.
- Feistner, A. T. C., & McGrew C., W. (1989). Food sharing in non-human primates: A critical review. *Perspectives in Primate Biology*.
- Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (Tursiops truncatus). *Marine Mammal Science*, 29(3), 203–225.
- Frye, D., Zelazo, P. D., Brooks, P. J., & Samuels, M. C. (1996). Inference and action in early causal reasoning. *Developmental Psychology*, 32(1), 120–131.
- Galef, B. G. (1999). Environmental enrichment for laboratory rodents: Animal welfare and the methods of science. *Journal of the Academy of Marketing Science*, 2(4), 267–280.
- Galhardo, L., Appleby, M. C., Waran, N. K., & dos Santos, M. E. (1996). Spontaneous activities of captive performing bottlenose dolphins (Tursiops truncatus). *Animal Welfare*, 5, 373–389.
- Gilbert, D. T., & Wilson, T. D. (2007). Prospection: Experiencing the Future. *Science*, *317*, 1351–1354.

Gopnik, A., & Schulz, L. (2007). Causal learning. Oxford, UK: Oxford University Press.

- Gotz, T., Verfuss, U. K., & Schnitzler, H.-U. (2006). "Eavesdropping" in wild roughtoothed dolphins (Steno bredanensis)? *Biology Letters*, 2, 5–7.
- Gowans, S., Würsig, B., & Karczmarski, L. (2007). The Social Structure and Strategies of Delphinids: Predictions Based on an Ecological Framework. *Advances in*

Marine Biology, 53, 195–294.

- Griffith, S. C., Pryke, S. R., & Buttemer, W. A. (2011). Constrained mate choice in social monogamy and the stress of having an unattractive partner. *Proceedings*. *Biological Sciences / The Royal Society*, 278(1719), 2798–805.
- Haidet, K. K., Tate, J., Divirgilio-Thomas, D., Kolanowski, A., & Happ, M. B. (2009).
 Methods to improve reliability of video recorded behavioral data. *Research in Nursing*, *32*(4), 465–474.
- Hanna, P. R., Frick, E. E., & Kuczaj, S. A. I. (2016). A Tool Use Task Proves Enriching for a Captive Sea Otter (Enhydra lutris). *Animal Behavior and Cognition*, 3(2), 88–94.
- Harley, H. E., Fellner, W., & Stamper, M. A. (2010). Cognitive Research with Dolphins (Tursiops truncatus) at Disney's The Seas: A Program for Enrichment, Science, Education, and Conservation. *International Journal of Comparative Psychology*, 23, 331–343.
- Harvey, B. N. (2015). The nature of social relationships in bottlenose Dolphins (Tursiops truncatus): associations and the role of affiliative, agonistic, and socio-sexual behaviors. (Masters thesis). University of Southern Mississippi. Retrieved from http://aquila.usm.edu/masters_theses/121/.
- Hauser, M. D., Kralik, J., & Botto-Mahan, C. (1999). Problem-solving and functional design features experiments on cotton-top tamarins, Saguinus oedipus oedipus. *Animal Behaviour*, 57, 565–582.
- Held, S. D. E., & Spinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, *81*, 891–899.

- Hill, H. M., Dietrich, S., Yeater, D., Mckinnon, M., Miller, M., Aibel, S., & Dove, A. (2015). Developing a Catalog of Socio-Sexual Behaviors of Beluga Whales (Delphinapterus leucas) in the Care of Humans. *Animal Behavior and Cognition*, 2(2), 105–123.
- Hill, H. M., Guarino, S., Crandall, S., Lenhart, E., & Dietrich, S. (2015). Young Belugas Diversify Adult Beluga (Delphinapterus leucas) Behavior. *Animal Behavior and Cognition*, 2(3), 267–284.
- Holyoak, K. J. (1995). Problem Solving. In E. E. Smith & D. O. Osherson (Eds.), *Thinking (Vol. 3)* (pp. 267–296). Cambridge, MA: MIT Press.
- Hoy, J. M., Murray, P. J., & Tribe, A. (2010). Thirty years later: Enrichment practices for captive mammals. *Zoo Biology*, 29, 303–316.
- Hunter, S. A., Bay, M. S., Martin, M. L., & Hatfield, J. S. (2002). Behavioral effects of environmental enrichment on harbor seals (Phoca vitulina concolor) and gray seals (Halichoerus grypus). *Zoo Biology*, 21, 375–387.
- Janik, V. M. (2000). Whistle Matching in Wild Bottlenose Dolphins (Tursiops truncatus). *Science*, 289, 1355–1357.
- Kuczaj, S. A. I., & Eskelinen, H. C. (2014). Why do dolphins play? *Animal Behavior and Cognition*, *1*(2), 113–127.
- Kuczaj, S. A. I., Gory, J. D., & Xitco, M. J. (2009). How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems. *Japanese Journal of Animal Psychology*, 59(1), 99–115.
- Kuczaj, S. A. I., Lacinak, T., Otto, F., Trone, M., Solangi, M., & Ramos, J. (2002).Keeping environmental enrichment enriching. *International Journal of*
Comparative Psychology, 15, 127–137.

- Kuczaj, S. A. I., Lacinak, T., & Turner, T. N. (1998). Environmental Enrichment for Marine Mammals at Sea World. In D. J. Shepherdson, J. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 314– 328). Washington DC: Smithsonian Institution Press.
- Kuczaj, S. A. I., Makecha, R., Trone, M., Paulis, 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. I., & Walker, R. T. (2012). Dolphin Problem Solving. In T. R. Zentall & E.
 A. Wasserman (Eds.), *The Oxford Handbook of Comparative Psychology* (pp. 736–756). New York, NY: Oxford University Press.
- Kuczaj, S. A. I., Xitco, M. J., & Gory, J. D. (2010). Can Dolphins Plan their Behavior? *International Journal of Comparative Psychology*, 23(4), 664–670.
- Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The choice to access outdoor areas affects the behavior of great apes. *Journal of Applied Animal Welfare Science*, 17, 185–197.
- Langbein, J., Siebert, K., & Nürnberg, G. (2009). On the use of an automated learning device by group-housed dwarf goats: Do goats seek cognitive challenges? *Applied Animal Behaviour Science*, 120, 150–158.
- Laule, G., & Desmond, T. (1998). Positive reinforcement training as an enrichment strategy. In D. J. Shepherdson, J. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 302–313). Washington DC:

Smithsonian Institution Press.

- Leavens, D., Aureli, F., Hopkins, W., & Hyatt, C. (2001). Effects of cognitive challenge on self-directed behaviors by chimpanzees (Pan troglodytes). *American Journal of Primatology*, 55(May), 1–14.
- Manteuffel, G., Langbein, J., & Puppe, B. (2009). From operant learning to cognitive enrichment in farm animal housing: Bases and applicability. *Animal Welfare*, 18, 87–95.
- Markowitz, H., & Line, S. W. (1989). Primate research models and environmental enrichment. In E. Segal (Ed.), *Housing, Care, and Psychological Well-Being for Laboratory Primates* (pp. 203–212). Park Ridge, NJ: Noyes Publications.
- Mason, G. J. (2010). Species differences in responses to captivity: stress, welfare and the comparative method. *Trends in Ecology & Evolution*, 25(12), 713–721.
- Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem-solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, 102(3–4), 246–261.
- Melfi, V. (2013). Is training zoo animals enriching? *Applied Animal Behaviour Science*, *147*(3–4), 299–305.
- Mellen, J., & MacPhee, M. S. (2001). Philosophy of Environmental Enrichment: Past, Present, and Future. Zoo Biology, 20, 211–226.
- Menzel, E. W. (1991). Chimpanzee (Pan troglodytes): Problem Seeking Versus the Birdin-hand, Least-effort Strategy. *Primates*, 32(4), 497–508.
- Miller, L. J., Pisacane, C. B., & Vicino, G. A. (2016). Relationship between behavioural diversity and faecal glucocorticoid metabolites: A case study with cheetahs

(Acinonyx jubatus). Animal Welfare, 25(3), 325–329.

- Miller, L. J., Zeigler-Hill, V., Mellen, J., Koeppel, J., Greer, T., & Kuczaj, S. A. I. (2013). Dolphin Shows and Interaction Programs: Benefits for Conservation Education? *Zoo Biology*, (32), 45–53.
- Miyata, H., & Fujita, K. (2012). Further tests of pigeons' (Columba livia) planning behavior using a computerized plus-shaped maze task. *Perceptual & Motor Skills: Learning and Memory*, 115(1), 27–42.
- Morgan, K. N., Line, S. W., & Markowitz, H. (1998). Zoos, enrichment, and the skeptical observer: the practical value of assessment. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 153–171). Washington DC: Smithsonian Institution Press.
- Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science*, *312*, 1038–1040.
- Murphy, E. S., Mcsweeney, F. K., & Kowal, B. P. (2003). Within-session decreases in operant responding as a function of pre-session feedings. *The Psychological Record*, 53, 313–326.
- 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*, 1–6.
- Newberry, R. C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, *44*, 229–243.
- Newton-Fisher, N. E. (2012). Animal Behaviour Pro. University of Kent. [Mobile application software]. Retrieved from http://itunes.apple.com

- Osvath, M. (2009). Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, *19*(5), 190–191.
- Osvath, M., & Osvath, H. (2008). Chimpanzee (Pan troglodytes) and orangutan (Pongo abelii) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition*, *11*, 661–674.
- Peet, R. K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics*, *5*(1), 285–307.
- Piaget, J. (1955). *The language and thought of a child*. New York, NY: World Publishing.
- Povinelli, D. J., & Cant, J. G. H. (1995). Arboreal clambering and the evolution of selfconception. *The Quarterly Review of Biology*, 70(4), 393–421.
- Procyk, E., & Joseph, J. P. (1996). Problem-solving and logical reasoning in the macaque monkey. *Behavioural Brain Research*, 82(1), 67–78.
- Pryor, K., & Shallenberger, I. K. (1998). Social structure in spotted dolphins (Stenella attenuata) in the tuna purse seine fishery in the eastern tropical pacific. In K.
 Pryor & K. S. Norris (Eds.), *Dolphin Societies: Discoveries and Puzzles* (pp. 161–198). Los Angeles: University of California Press.
- Puppe, B., Ernst, K., Schon, P. C., & Manteuffel, G. (2007). Cognitive enrichment affects behavioural reactivity in domestic pigs. *Applied Animal Behaviour Science*, 105, 75–86.
- Quirke, T., & O'Riordan, R. M. (2012). Evaluation and Interpretation of the Effects of Environmental Enrichment Utilizing Varying Degrees of Sampling Effort. *Zoo Biology*, 1–11.

- R Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Reader, S. M., & Laland, K. N. (2003). Animal Innovation. Oxford, UK: Oxford University Press.
- Reamer, L. A., Haller, R. L., Thiele, E. J., Freeman, H. D., Lambeth, S. P., & Schapiro,
 S. J. (2014). Factors affecting initial training success of blood glucose testing in
 captive chimpanzees (Pan troglodytes): Chimpanzee diabetic treatment training. *Zoo Biology*, 33(3), 212–220.
- Roberts, W. (2012). Evidence for future cognition in animals. *Learning and Motivation*, *43*, 169–180.
- Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (Ursus maritimus). *Behavioural Processes*, 73(1), 117–120.
- Ross, S. R. (2010). How cognitive studies help shape our obligations for the ethical care of chimpanzees. In E. V. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives* (pp. 309–319). Chicago, IL: The University of Chicago Press.
- Sambrook, T. D., & Buchanan-Smith, H. M. (1997). Control and Complexity in Novel Object Enrichment. *Animal Welfare*, *6*, 207–216.

Samuelson, M. M., Lauderdale, L. K., Pulis, K., Solangi, M., Hoffland, T., & Lyn, H.
(2017). Olfactory Enrichment in California Sea Lions (Zalophus californianus):
An Effective Tool for Captive Welfare? *Journal of Applied Animal Welfare Science*, 20(1), 75–85.

Shannon, C. E., & Weaver, W. (1949). The mathematical theory of communication.

Urbana, IL: University of Illinois Press.

- Shepherdson, D. J., Mellen, J., & Hutchins, M. (1998). Second nature: Environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press.
- Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71(8), 1494–1499.
- Smith, B. P., & Litchfield, C. a. (2010). An empirical case study examining effectiveness of environmental enrichment in two captive Australian Sea Lions (Neophoca cinerea). *Journal of Applied Animal Welfare Science*, 13, 103–122.
- Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge Carrying by Dolphins (Delphinidae, Tursiops sp.): A Foraging Specialization Involving Tool Use? *Ethology*, 103, 454–465.
- Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences*, *30*(3), 299–313.
- Swaisgood, 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 Biology*, 24, 499–518.
- Swaisgood, R. R., White, A. M., Zhou, X. P., Zhang, H. M., Zhang, G. Q., Wei, R. P., ... Lindburg, D. G. (2001). A quantitative assessment of the efficacy of an environmental enrichment program for giant pandas. *Animal Behaviour*, 61, 447– 457.

Tarou, L. R., & Bashaw, M. J. (2007). Maximizing the effectiveness of environmental

enrichment: Suggestions from the experimental analysis of behavior. *Applied Animal Behaviour Science*, *102*, 189–204.

- Tecwyn, E. C., Thorpe, S. K. S., & Chappell, J. (2012). What cognitive strategies do orangutans (Pongo pygmaeus) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? *Animal Cognition*, 15, 121–133.
- Tolman, E. C. (1932). *Purposive behavior in animals and men*. Berkeley, CA: University of California Press.
- van Hooff, J. A. R. A. M., & Lukkenaar, B. (2015). Captive chimpanzee takes down a drone: tool use toward a flying object. *Primates*, *56*(4), 289–292.
- Völter, C. J., & Call, J. (2012). Problem-solving in great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo abelii): the effect of visual feedback.
 Animal Cognition, 15(5), 923–936.
- Waples, K. A., & Gales, N. J. (2002). Evaluating and minimizing social stress in the care of captive bottlenose dolphins (Tursiops aduncus). *Zoo Biology*, 21, 5–26.
- Washburn, M. F. (1936). The animal mind. New York, NY: Macmillan Company.
- Watson, S. L., Shively, C. A., & Voytko, M. Lou. (1999). Can puzzle feeders be used as cognitive screening instruments? Differential performance of young and aged female monkeys on a puzzle feeder task. *American Journal of Primatology*, 49(2), 195–202.
- Wells, R. S. (2009). Learning from nature: Bottlenose dolphin care and husbandry. Zoo Biology, 28, 635–651.
- Wergård, E.-M., Westlund, K., Spångberg, M., Fredlund, H., & Forkman, B. (2016). Training success in group-housed long-tailed macaques (Macaca fascicularis) is

better explained by personality than by social rank. *Applied Animal Behaviour Science*, 1–7.

- White, B. C., Houser, L. A., Fuller, J. A., Taylor, S., & Elliott, J. L. (2003). Activity-Based Exhibition of Five Mammalian Species: Evaluation of Behavioral Changes. *Zoo Biology*, 22, 269–285.
- Wrangham, R. W. (1975). The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Cambridge, UK: University of Cambridge.