

Efficacy of an interactive apparatus as environmental enrichment for common bottlenose dolphins (*Tursiops truncatus*)

LK Lauderdale^{*†‡} and LJ Miller[‡]

[†] Department of Psychology, University of Southern Mississippi, 118 College Drive, Hattiesburg, MS 39406, USA

[‡] Chicago Zoological Society, Brookfield Zoo, 3300 Golf Road, Brookfield, IL 60513, USA

* Contact for correspondence: lisa.lauderdale@czs.org

Abstract

Environmental enrichment is a key component in improving the psychological and physiological well-being of animals under professional care. Environmental enrichment involves the addition of stimuli, including objects and cognitive challenges, into the environment in order to increase species-specific behaviour and provide opportunities for choice and control. The effectiveness of enrichment should be evaluated on a case-by-case basis to determine if the desired result has been achieved. Environmental enrichment devices (EEDs) can be utilised to present novel problems to animals under professional care. Here, a submerged interactive cognitive apparatus was presented to eight bottlenose dolphins (*Tursiops truncatus*) five days a week for 18 weeks and behavioural indicators of animal welfare assessed. As a group, dolphins spent more time in social swims compared to solitary swims and more time at the bottom of the habitat than the middle or top throughout the day, even when the apparatus was not immediately available. Individuals' differences were apparent in the type and amount of engagement with the apparatus. Three dolphins engaged with the apparatus by solving it or consuming the reward. Two dolphins, D4 and D8, engaged simultaneously with the apparatus and participated in more social swimming with each other. D4 solved the interactive apparatus and engaged in more social active and solitary active behaviours. D1 and D4 increased their use of the bottom of the habitat. This study is the first report of underwater enrichment increasing dolphins time at depth throughout the day even when the enrichment device is not available. The interactive apparatus was an effective form of enrichment for dolphins participating in successful trials.

Keywords: animal welfare, bottlenose dolphin, enrichment, environmental enrichment device, habitat use, social enrichment

Introduction

Zoos and aquaria often implement environmental enrichment programmes to improve the welfare of animals under their care (Kuczaj *et al* 2002; Harley *et al* 2010). Environmental enrichment involves the addition of stimuli to the environment in order to increase species-specific behaviour and provide opportunities for choice and control (Chamove 1989; White *et al* 2003). Environmental enrichment can comprise a variety of different activities (for a review, see Hoy *et al* 2010), including the addition of objects to a habitat (eg television, balls, and underwater mazes; Newberry 1995; Swaisgood & Shepherdson 2005; Wells 2009; Clark *et al* 2013; Melfi 2013), novel scents (Fay & Miller 2015; Samuelson *et al* 2017), training (Brando 2012), and strategic social changes made with the goal of improving welfare (Hill *et al* 2015b).

Enrichment programmes focus on increasing positive indicators of welfare, such as increased behavioural diversity, affiliative behaviours, and habitat usage (Kuczaj *et al* 1998; Swaisgood & Shepherdson 2005; Wells 2009; Mason 2010; Miller *et al* 2016) and can result in decreased indicators of

negative welfare, such as stereotypic and abnormal levels of aggressive behaviours (Carlstead 1998; Waples & Gales 2002; White *et al* 2003). Ethological and physiological studies examining the efficacy of environmental enrichment programmes should be conducted to determine the effectiveness of these enrichment devices in increasing positive welfare for the animals (Kuczaj *et al* 2002; Clegg *et al* 2015). The enrichment value depends on the audience, as not all environmental enrichment devices (EEDs) are equally effective for bottlenose 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 (Mellen & MacPhee 2001; Delfour & Beyer 2012). Therefore, the effectiveness of enrichment initiatives should be evaluated to determine the type and quantity necessary to produce the desired result (Morgan *et al* 1998; Galef 1999). Successful cognitive enrichment tasks must: (i) require animals to engage their cognitive skills to solve problems or control the environment; and (ii) result in positive changes in validated measures of well-being (Clark 2011).

Table 1 Demographic information on participants.

Dolphin	Age	Group	Sex	Mother-calf dyads
D2	11	1	Female	–
D3	2	1	Male	–
D6	13	1	Female	–
D7	14	1	Female	–
D1	30	2	Female	Mother of D4
D4	1	2	Female	Calf of D1
D5	2	2	Male	Calf of D8
D8	34	2	Female	Mother of D5

Behavioural diversity and activity level have been used as a measure of welfare (Galhardo *et al* 1996), and recent efforts have worked toward validating behavioural diversity as an indicator of welfare using physiological measures (Miller *et al* 2016). Several studies have shown an increase in behavioural diversity and active behaviours when animals are presented with various types of environmental enrichment (Shepherdson *et al* 1993; Garner *et al* 2003; Schneider *et al* 2014). For example, giant pandas (*Ailuropoda melanoleuca*) presented with food and non-food enrichment items spent significantly more time active and engaged in a greater variety of behaviours (Swaigood *et al* 2001), and implementing unpredictability with Malayan sun bears (*Helarctos malayanus*) led to a higher diversity of foraging behaviours (Schneider *et al* 2014). Consistently, reductions in social behaviour and activity levels have been associated with increased cortisol levels, reduced appetite, and illness in dolphins (Waples & Gales 2002). Behavioural diversity and activity levels likely can be used to identify when the animal is in a positive state.

Affiliative behaviours, such as social play, rubbing, and synchronous swimming have been considered variables indicative of positive welfare, leading to health benefits (Kuczaj *et al* 2006; Held & Spinka 2011; Clark *et al* 2013; Hill *et al* 2015a,b). Wild dolphins have dynamic social lives in fission-fusion societies, where they learn to employ a wide variety of foraging strategies (Similä & Ugarte 1993; Smolker *et al* 1997; Duffy-Echevarria *et al* 2008). Some socially learned foraging strategies are co-operative and involve synchronous behaviours, which aid in social cohesion (Connor *et al* 2006; Fellner *et al* 2013). Similarly, co-operative play in dolphins is particularly important in acquiring information about conspecifics and developing social skills (Kuczaj & Eskelinen 2014). Social play decreases in unfavourable conditions and increases when environmental enrichment is present (Serres & Delfour 2017). After training sessions, rates of social play and interactions with environmental enrichment are higher (Serres & Delfour 2017; Perez *et al* 2018).

Habitat utilisation, as a proxy for exploration, has been used an indicator of welfare when assessing the efficacy of enrichment. For example, food-hiding programmes in the enclosures of land animals (Charmoy *et al* 2015), and the introduction of novel scents to sea lions (*Zalophus californianus*) (Samuelson *et al* 2017) have successfully increased habitat usage. Dolphins under professional 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 (Clark *et al* 2013).

Research on enrichment devices has mainly focused on non-interactive objects (Delfour & Beyer 2012; Clark *et al* 2013). These are effective in increasing species-specific behaviour and decreasing stereotypic behaviour (Hunter *et al* 2002; Smith & Litchfield 2010; Delfour & Beyer 2012). Providing cognitively challenging enrichment may produce longer-lasting benefits and expand overall knowledge of dolphin cognition (Meehan & Mench 2007; Harley *et al* 2010). Cognitive challenges have benefitted the well-being of farm animals by increasing locomotive behaviour and reducing fear behaviours (Puppe *et al* 2007). They are also effective forms of enrichment for dolphins by increasing social behaviours, play behaviours, and amount of time spent underwater (Clark 2011, 2013).

The purpose of the present study was to examine the impact of a submerged problem-solving apparatus by assessing behavioural indicators of animal welfare.

Materials and methods

Ethical approval

The study protocol was approved by the University of Southern Mississippi Institutional Animal Care and Use Committee (no 16052607).

Methods

Eight common bottlenose dolphins, housed at the Brookfield Zoo in Brookfield, Illinois, USA (41° 49' 26.04", 87° 51' 6.12") were observed in order to examine the enrichment efficacy of a submerged interactive apparatus (SIA) over a ten-month period. The group consisted of one female/male mother-calf dyad, one female/female mother-calf dyad, three sub-adult females, and one male calf (Table 1). The habitat consisted of four interconnected areas: an oblong front area (33.5 × 12.2 × 6.7 m; length × width × depth), two circular rear areas (10.7 × 4.3 m; diameter × depth), and a medical area (7.6 × 2.4 m; diameter × depth).

The SIA consisted of a clear Lexan (ie, polycarbonate plastic) box, submerged 0.6 m beneath the water's surface, containing a shelf that was lowered to release a food reward (four fish) when a specific amount of weight was placed inside (for a detailed description of the SIA, see Lauderdale & Miller 2019). Sinking weights were dispersed at a designated location at the bottom of the habitat in each area based on the study condition. Dolphins were tested in two groups

of four, with the two mother-calf dyads in Group 2 (Table 1). The SIA was presented five days a week between 1200 and 1300h, directly following a training session during which feeding took place. The opportunity for trainer interaction was not normally available during this time-period. Dolphins received their normal daily enrichment (eg balls, buoys, water hoses, hula hoops, etc) throughout the study.

Behavioural observations were collected for 12 weeks prior to the introduction of an SIA (ie, pre-treatment phase), for the 18 weeks the SIA was presented (ie, treatment phase), and for 12 weeks after the SIA was no longer presented (ie, post-treatment phase). A total of 18 h of behavioural observations were recorded each week. Real-time, direct observations were conducted from underwater viewing windows and recorded using the iOSmobile application, Animal Behaviour Pro. Observations were collected on a randomised, counterbalanced schedule, five days a week, between the hours of 0630–1800h. Data were not collected during formal presentations, training sessions, or during trials with the apparatus. Behavioural data were gathered following a protocol of consecutive 15-min focal follows for each dolphin. Continuous sampling was used to record behaviour events (eg interaction with conspecifics, objects and trainers/guests). Instantaneous sampling of swim state and location were recorded at 60-s intervals. At each social swim state sample point, the identification of the participating dolphins was recorded. Behaviour events, swim states and locations are operationally defined and categorised in Appendix 1 (see supplementary material to papers published in *Animal Welfare*: <https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material>). Operational definitions are adapted, in part, from Dudzinski (1996), Harvey (2015), and Hill *et al* (2015a).

A combination of live observation and video recordings were used to ensure reliability. Inter-observer agreement (IOA) was evaluated for 16 live observation periods (two pre- and two post-treatment observations per animal). IOA was calculated with Pearson's correlation coefficient and Cohen's kappa and was achieved across subjects, with both coders reaching at least 80% reliability for continuous and instantaneous data (Haidet *et al* 2009). In order to calculate intra-observer reliability, three 1-h videos were scored prior to the beginning of the pre-treatment, treatment, and post-treatment phases. Reliability was calculated with Pearson's correlation coefficient and Cohen's kappa and was at least 80% reliability for continuous and instantaneous data.

Due to the small sample size, all analyses were conducted using non-parametric tests and differences considered significant at $P < 0.05$. Data were analysed using R and SPSS and partitioned into groups of nine consecutive observations in order to create blocks. Average time spent in each swim state and location for each block and phase (ie, pre-treatment, treatment, or post-treatment) were calculated. To examine differences in location and swim state, the total number of occurrences in each category was summed and divided by the total number of visible scans for each dolphin per session. To assess differences in

behaviour events using the continuous samples, the total number of events in each category (ie, social active, social agonistic, social sexual, and solitary active) was summed and divided by the total number of minutes visible. Differences were compared between pre-treatment, treatment, and post-treatment phases using a Friedman's test. In the case of overall significance ($P < 0.05$), a Wilcoxon Signed Ranks test was calculated.

To determine the significant changes in behaviour, location, and swim state diversity in response to the SIA, the Shannon's diversity index (Shannon & Weaver 1949) was calculated for each variable, since it is able to identify subtle changes in behavioural diversity (DeJong 1975). Behavioural diversity is notated in H values, with higher values indicating a greater number of behaviours and/or an even distribution of behaviours (Peet 1974). The Shannon index (H) is calculated as:

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

where p_i is the proportion of the behaviour category. An absence of behaviours 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 Friedman's test. In the case of overall significance ($P < 0.05$), a Wilcoxon Signed Ranks test was calculated.

Phase design randomisation tests were used to compare the treatment phase to the pre- and post-treatment phases for individual dolphins (Dugard & Todman 2012; Kratochwill 2013). Phase design randomisation tests are commonly employed with ABA design experiments (Dugard & Todman 2012). In order to complete these tests, data were grouped into two phases: treatment and non-treatment phases. Pre- and post-treatment phases were grouped into a single phase collectively referred to as the non-treatment phase. For dolphins with significant changes in social behaviour as indicated by the randomisation tests, social association changes (ie, rate of social swim states specific dolphins were observed together in) were investigated by calculating an effect size; Tau-U. This is a non-parametric effect size calculation for evaluating non-overlap data between two phases (Parker *et al* 2011). Tau-U effect size scores ranging from 0.00–0.20 are considered small effects, scores ranging from 0.20–0.60 are considered moderate effects, scores ranging from 0.60–0.80 are considered large effects, and scores above 0.80 are considered a very large effect (Vannest & Ninci 2015).

Results

Dolphins spent 52.1% of their time in social swims during the pre-treatment phase, 58.2% in the treatment phase, and 51.5% in the post-treatment phase. The mean proportion of time spent in social swim states was statistically significant ($\chi^2_{[2, n=8]} = 7.00$; $P = 0.03$). There were significantly more social swims in the treatment compared to the pre-treatment ($Z = -2.10$; $P = 0.04$) and post-treatment phases ($Z = -2.52$;

Table 2 Mean difference values for behaviour during treatment and non-treatment phases.

Dolphin	Social active	Social	Social sexual	Solitary
D1	0.04	0.00	0.00	0.04
D2	0.07	0.00	0.00	-0.04
D3	-0.19	-0.01	0.09	-0.06
D4	0.31*	0.02	0.04	0.18*
D5	-0.38	-0.02	0.00	-0.06
D6	-0.02	0.00	0.01	-0.04
D7	-0.12	0.00	0.00	-0.06
D8	-0.08	0.00	-0.03	-0.04

Negative numbers indicate a decrease and positive numbers indicate an increase. * $P < 0.05$, two-tailed.

Table 3 Mean difference values for location and swim state during treatment and non-treatment phases.

Dolphin	Top	Middle	Bottom	Solitary swim	Social swim
D1	-0.08*	0.02	0.06*	-0.06	0.06
D2	-0.13	-0.01	0.14	-0.10	0.09
D3	-0.02	-0.03	0.05	0.03	0.00
D4	-0.04	-0.01	0.05*	0.01	-0.01
D5	-0.05	0.00	0.05	-0.06	0.05
D6	-0.09	0.00	0.10	-0.13	0.12
D7	-0.10	0.03	0.07	-0.11	0.11
D8	-0.04	0.01	0.04	-0.12*	0.12*

Negative numbers indicate a decrease and a positive numbers indicate an increase. * $P < 0.05$, two-tailed.

$P = 0.01$). Dolphins predominantly engaged in social active (group average = 58.9% of observed behaviours) and solitary active behaviours (group average = 28.9% of observed behaviours) in all conditions. The dolphins spent significantly more time at the bottom of the habitat ($\chi^2_{[2, n=8]} = 9.00$; $P = 0.01$) in the treatment phase when compared to the post-treatment phase ($Z = -2.52$; $P = 0.01$). They spent significantly less time at the top of the habitat ($\chi^2_{[2, n=8]} = 10.75$; $P = 0.01$) in the treatment phase when compared to the pre-treatment ($Z = -2.10$; $P = 0.04$) and post-treatment phases ($Z = -2.52$; $P = 0.01$). They spent 32.4% of their time at the bottom of the habitat in the pre-treatment phase, 37.4% in the treatment phase, and 28.8% in the post-treatment phase. Shannon's diversity index phase values ranged from 0.65–0.91 for behaviour, 0.61–0.93 for swim state, and 1.16–1.29 for location. As a group, there were no significant differences for diversity of behaviour ($\chi^2_{[2, n=8]} = 0.75$; $P = 0.79$), diversity of swim states ($\chi^2_{[2, n=8]} = 1.00$; $P = 0.65$), or location ($\chi^2_{[2, n=8]} = 0.75$; $P = 0.79$).

Randomisation tests were completed to assess individual differences in behaviour change because each dolphin participated with the SIA in a different manner and amount. None of the dolphins in Group 1 (D2, D3, D5, and D7) were able to solve the SIA despite continuous attempts to do so via other methods (eg pushing). In Group 2, D4 solved 100% of the SIA-completed trials. D1 consumed 18.5%, D4 6.5%, and D8 75.0% of the total amount of food reward available.

Mean differences for individuals from the phase design randomisation tests are shown in Tables 2 and 3. D4 engaged in social active and solitary active behaviours significantly more during the treatment when compared to the non-treatment phase (social active: mean difference = 0.21; $P = 0.04$, solitary active: mean difference = 0.18; $P = 0.02$). D8 displayed significantly more social swim states and fewer solitary swim states during the treatment when compared to the non-treatment phase (social swims: mean difference = 0.12; $P = 0.02$, solitary swims: mean difference = 0.12; $P = 0.02$). Two subjects, D1 and D4, spent significantly more time at the bottom of the habitat (D1: mean difference = 0.06; $P = 0.04$, D4: mean difference = 0.05; $P = 0.05$) during the treatment when compared to the non-treatment phase. D1 spent significantly less time at the top of the habitat (mean difference = 0.08; $P = 0.05$).

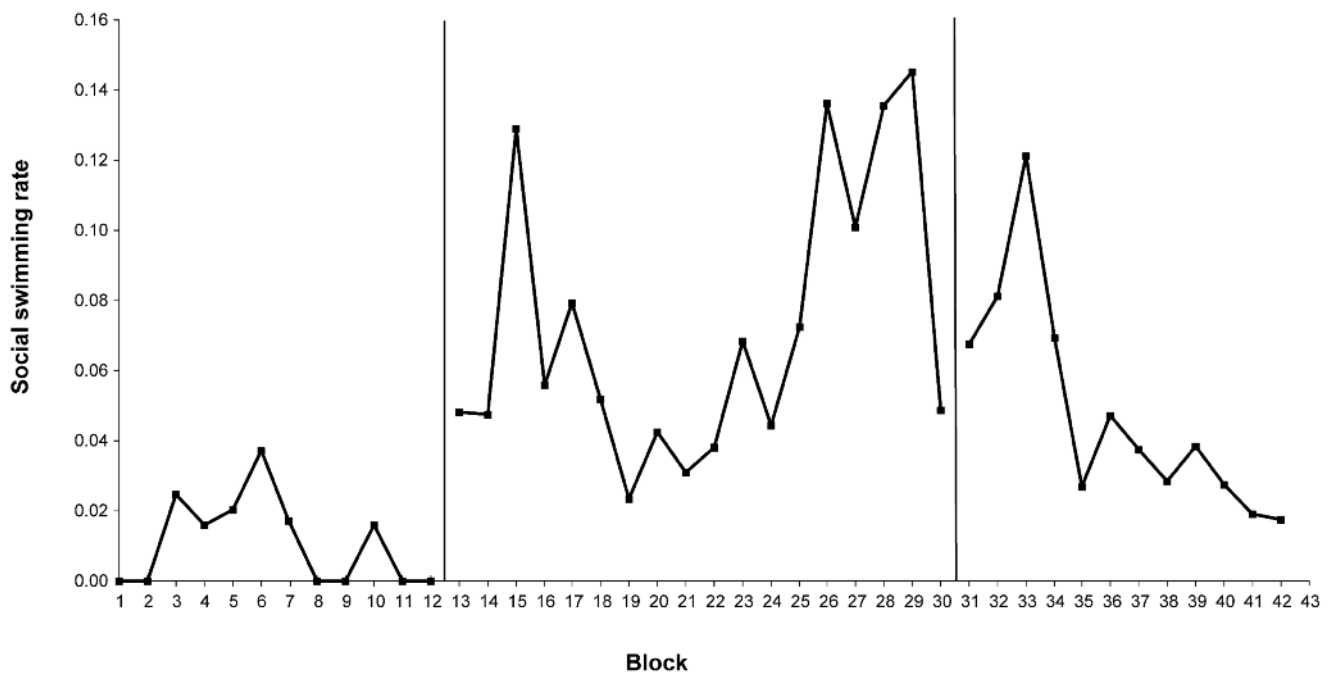
Tau-U effect size calculations for D4 and D8's rate of social swimming between phases indicated very large effects of the treatment when compared to pre-treatment (Tau = 0.97) and the pre- compared when compared to post-treatment (Tau = 0.88). There were moderate effects between the treatment and post-treatment (Tau = 0.44). The rates of social swimming between D4 and D8 are shown in Figure 1.

Discussion

The present study showed usage of a submerged interactive apparatus and the accompanying sinking weights to be associated with positive behavioural change throughout the day even when the SIA and weights were not available. During the time-period when SIA trials were conducted, the three dolphins who either solved the SIA and/or consumed the food reward exhibited an increase in one or more likely indicators of positive welfare. D1 and D8 consumed the majority of the food reward while D4 solved the SIA. Individual differences in the amount and type of interaction with EEDs illustrates the importance of assessing the efficacy of enrichment for each individual (Delfour & Beyer 2012).

Synchronous swimming in close proximity is considered an affiliative behaviour indicative of positive welfare for bottlenose dolphins (Connor *et al* 2000). D4 and D8 spent more time in social swim states together during the treatment phase despite being an unrelated adult-calf pair. The simultaneous engagement with the SIA may have enhanced the social bond between these individuals. It is possible that D4 strengthened her relationship with D8 through solving the enrichment device, thereby enabling herself to be associated with a food reward to D8, who consumed it. It is also possible that D4 was participating in a form of prosocial behaviour. When offered a choice

Figure 1



Rates of social swimming between dolphins, D4 and D8.

between a prosocial or a selfish act, dolphins favour the former which provides both themselves and their conspecific with enrichment without request from the conspecific (Nakahara *et al* 2017).

Habitat utilisation, as a proxy for exploration, has been used as a potential indicator of positive welfare when assessing the efficacy of enrichment (Leighty *et al* 2010; Blowers *et al* 2012; Hunter *et al* 2014). As dolphins have access to three dimensions of their environments, compared to most terrestrial mammals that have access to two, it is important to include assessments of depth usage when investigating how dolphins use their habitats. Underwater enrichment has been shown to increase the amount of time dolphins spend at the same depth as the EED while the enrichment is present (Clark *et al* 2013). The sinking weights used with the apparatus required dolphins to navigate the entire depth of their habitat in order to participate, which may have increased their exploratory behaviours. Even when the SIA and weights were not in the water, D1 and D4 continued to spend less time at the top of the habitat and more time at the bottom during the treatment phase than in other phases. This study is the first to report underwater enrichment increasing dolphins time at depth throughout the day even when the enrichment device is not available.

Non-aggressive social interactions in the absence of fitness threats have been identified as indicators of positive welfare (Held & Spinka 2011). Interactive enrichment has been shown to stimulate social interactions when the enrichment is present (Clark *et al* 2013). D4 engaged in more social and more solitary active behaviours when the SIA was not present indicating that the opportunity to

interact with the apparatus prompted more positive social interactions throughout the day.

While the SIA appears to have been enriching, the presence of the researcher and assisting trainer or the additional time spent with the trainer during the trials may also have influenced the dolphins' behaviour. Human interaction is enriching even when no objects are present (Eskelinen *et al* 2015). Trials took place in a 1-h period during which human-dolphin interactions did not normally occur. It is possible that the increased activity and human interaction could have provided additional enrichment. However, each participant received an increase in human interaction during the treatment period but only D1, D4, and D8, who most readily directly interacted with the SIA, showed altered behaviour. Therefore, the SIA was more likely responsible for the changes in behaviour rather than an increase in human interaction.

Animal welfare implications and conclusion

The current study aimed to examine the impact of a challenging cognitive apparatus. The SIA promoted positive welfare for dolphins who participated in successful trials by increasing their social behaviours, increasing use of the bottom of the habitat, and promoting social cohesion between dolphins. The dolphins were able to choose their level of engagement with the device. Individual differences were observed in the type and amount of interaction with the apparatus which highlight the importance of evaluating potential enrichment devices at the individual level. EEDs, such as the SIA here, may also promote social bonding between individuals interacting with the SIA together. The

increase in social swimming between two unrelated dolphins interacting with the SIA concurrently, indicated that that EEDs may strengthen social bonds without co-operation. Importantly, this increase in social swimming behaviours occurred when the SIA was not being presented, suggesting that time-limited enrichment that includes social interactions may improve overall social cohesion. These two dolphins showed an increase in their habitat use by spending more time at the bottom of the habitat. Further, the dolphin who solved the cognitive challenge exhibited an increase in social and solitary active behaviours.

Environmental enrichment is a crucial component of improving the welfare of marine mammals (Swaigood *et al* 2001; Shepherdson *et al* 2005). Information gained from this study can be used to aid in developing environmental enrichment programmes, designing new cognitive challenge devices, and managing social groups. Future research should focus on individual differences in participation amount and type and the effect these have on behaviour. In addition, more research is needed to better understand the effects of enrichment that promotes social interactions and the impact of dominance hierarchy on social bonding.

Acknowledgements

The authors would like to thank Dr Stan Kuczaj for providing the foundation for this study and his guidance during its initial stages. We would also like to thank the Chicago Zoological Society, Rita Stacey, Bill Zeigler, Sarah Breen-Bartecki, and the Seven Seas animal care specialists for their assistance during data collection and their support of this project.

References

- Blowers TE, Waterman JM, Kuhar CW and Bettinger TL** 2012 Female Nile hippopotamus (*Hippopotamus amphibius*) space use in a naturalistic exhibit. *Zoo Biology* 2: 129-136. <https://doi.org/10.1002/zoo.20366>
- Brando SI** 2012 Animal learning and training: implications for animal welfare. *The Veterinary Clinics of North America. Exotic Animal Practice* 15: 387-398. <https://doi.org/10.1016/j.cvex.2012.06.008>
- Carlstead K** 1998 Determining the causes of stereotypic behaviours in zoo carnivores: toward appropriate enrichment strategies. In: Shepherdson DJ, Mellen J and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 172-183. Smithsonian Institution Press: Washington DC, USA
- Chamove AS** 1989 Environmental enrichment: a review. *Animal Technology* 40(3): 155-178
- Charmoy K, Sullivan T and Miller LJ** 2015 Impact of different forms of environmental enrichment on foraging and activity levels in gorillas (*Gorilla gorilla gorilla*). *Animal Behavior and Cognition* 2: 233-240. <https://doi.org/10.12966/abc.08.03.2015>
- Clark FE** 2011 Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science* 135: 1-12. <https://doi.org/10.1016/j.applanim.2011.10.010>
- Clark FE** 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 FE, Davies SL, Madigan AW, Warner AJ and Kuczaj SA** 2013 Cognitive enrichment for bottlenose dolphins (*Tursiops truncatus*): Evaluation of a novel underwater maze device. *Zoo Biology* 32: 608-619. <https://doi.org/10.1002/zoo.21096>
- Clegg ILK, Borger-Turner JL and Eskelinen HC** 2015 C-Well: The development of welfare assessment measures and protocols for captive bottlenose dolphin (*Tursiops truncatus*). *Animal Welfare* 24: 267-282. <https://doi.org/10.7120/09627286.24.3.267>
- Connor RC, Smolker R and Bejder L** 2006 Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour* 72: 1371-1378. <https://doi.org/10.1016/j.anbehav.2006.03.014>
- Connor RC, Wells RS, Mann J and Read AJ** 2000 The bottlenose dolphin: social relationships in a fission-fusion society In: Mann J, Connor R, Tyack PL and Whitehead H (eds) *Cetacean Societies: Field Studies of Dolphins and Whales*. The University of Chicago Press: Chicago, USA
- DeJong TM** 1975 A comparison of three diversity indices based on their components of richness and evenness. *Oikos* 26: 222-227. <https://doi.org/10.2307/3543712>
- Delfour F and Beyer H** 2012 Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology* 31: 137-150. <https://doi.org/10.1002/zoo.20383>
- Dudzinski KM** 1996 *Communication and behavior in the Atlantic spotted dolphins (Stenella frontalis): Relationships between vocal and behavioral activities*. Texas A&M University: Texas, USA
- Duffy-Echevarria EE, Connor RC and St Aubin DJ** 2008 Observations of strand-feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South Carolina. *Marine Mammal Science* 24: 202-206. <https://doi.org/10.1111/j.1748-7692.2007.00151.x>
- Dugard P and Todman J** 2012 *Single-case and Small-n Experimental Designs: A Practical Guide to Randomization Tests*. Routledge Academics: New York, NY, USA. <https://doi.org/10.4324/9780203180938>
- Eskelinen HC, Winship KA and Borger-Turner JL** 2015 Sex, age, and individual differences in bottlenose dolphins (*Tursiops truncatus*) in response to environmental enrichment. *Animal Behavior and Cognition* 2: 241-253. <https://doi.org/10.12966/abc.08.04.2015>
- Fay C and Miller LJ** 2015 Utilising scents as environmental enrichment: Preference assessment and application with Rothschild giraffe. *Animal Behavior and Cognition* 2: 285-291. <https://doi.org/10.12966/abc.08.07.2015>
- Fellner W, Bauer GB, Stamper SA, Losch BA and Dahood A** 2013 The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science* 29: 203-225. <https://doi.org/10.1111/j.1748-7692.2012.00609.x>
- Galef BG** 1999 Environmental enrichment for laboratory rodents: Animal welfare and the methods of science. *Journal of the Academy of Marketing Science* 2: 267-280. https://doi.org/10.1207/s15327604jaws0204_2
- Galhardo L, Appleby MC, Waran NK and dos Santos ME** 1996 Spontaneous activities of captive performing bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare* 5: 373-389
- Garner JP, Mason GJ and Smith R** 2003 Stereotypic route-tracing in experimentally caged songbirds correlates with general behavioural disinhibition. *Animal Behaviour* 66: 711-727. <https://doi.org/10.1006/anbe.2002.2254>

- Haidet KK, Tate J, Divirgilio-Thomas D, Kolanowski A and Happ MB** 2009 Methods to improve reliability of video recorded behavioral data. *Research in Nursing* 32: 465-474. <https://doi.org/10.1002/nur.20334>
- Harley HE, Fellner W and Stamper MA** 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 BN** 2015 *The nature of social relationships in bottlenose dolphins (Tursiops truncatus): associations and the role of affiliative, agonistic, and socio-sexual behaviors*. University of Southern Mississippi, USA
- Held SD and Spinka M** 2011 Animal play and animal welfare. *Animal Behaviour* 81: 891-899. <https://doi.org/10.1016/j.anbehav.2011.01.007>
- Hill HM, Dietrich S, Yeater D, McKinnon M, Miller M, Aibel S and Dove A** 2015a Developing a catalogue of socio-sexual behaviors of beluga whales (*Delphinapterus leucas*) in the care of humans. *Animal Behavior and Cognition* 2: 105-123. <https://doi.org/10.12966/abc.05.01.2015>
- Hill HM, Guarino S, Crandall S, Lenhart E and Dietrich S** 2015b Young belugas diversify adult beluga (*Delphinapterus leucas*) behavior. *Animal Behavior and Cognition* 2: 267-284. <https://doi.org/10.12966/abc.08.06.2015>
- Hoy JM, Murray PJ and Tribe A** 2010 Thirty years later: Enrichment practices for captive mammals. *Zoo Biology* 29: 303-316. <https://doi.org/10.1002/zoo.20254>
- Hunter SA, Bay MS, Martin ML and Hatfield JS** 2002 Behavioral effects of environmental enrichment on harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*). *Zoo Biology* 21: 375-387. <https://doi.org/10.1002/zoo.10042>
- Hunter SC, Gusset M, Miller LJ and Somers MJ** 2014 Space use as an indicator of enclosure appropriateness in African wild dogs (*Lycaon pictus*). *Journal of Applied Animal Welfare Science* 17(2): 98-110. <https://doi.org/10.1080/10888705.2014.884401>
- Kratochwill TR** 2013 *Single Subject Research: Strategies for Evaluating Change*. Academic Press: New York, USA
- Kuczaj SA and Eskelinen HC** 2014 Why do dolphins play? *Animal Behavior and Cognition* 1: 113-127. <https://doi.org/10.12966/abc.05.03.2014>
- Kuczaj SA, Lacinak T, Otto F, Trone M, Solangi M and Ramos J** 2002 Keeping environmental enrichment enriching. *International Journal of Comparative Psychology* 15: 127-137
- Kuczaj SA, Lacinak T and Turner TN** 1998 Environmental enrichment for marine mammals at Sea World. In: Shepherdson DJ, Mellen J and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 314-328. Smithsonian Institution Press: Washington DC, USA
- Kuczaj SA, Makecha R, Trone M, Paulis RD and Ramos JA** 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
- Lauderdale LK and Miller LJ** 2019 Common bottlenose dolphin (*Tursiops truncatus*) problem-solving strategies in response to a novel interactive apparatus. *Behavioural Processes* 169: 103990. <https://doi.org/10.1016/j.beproc.2019.103990>
- Leighty KA, Soltis J and Savage A** 2010 GPS assessment of the use of exhibit space and resources by African elephants (*Loxodonta africana*). *Zoo Biology* 29(2): 210-220. <https://doi.org/10.1002/zoo.20250>
- Mason GJ** 2010 Species differences in responses to captivity: stress, welfare and the comparative method. *Trends in Ecology & Evolution* 25: 713-721. <https://doi.org/10.1016/j.tree.2010.08.011>
- Meehan CL and Mench JA** 2007 The challenge of challenge: Can problem-solving opportunities enhance animal welfare? *Applied Animal Behaviour Science* 102: 246-261. <https://doi.org/10.1016/j.applanim.2006.05.031>
- Melfi V** 2013 Is training zoo animals enriching? *Applied Animal Behaviour Science* 147: 299-305. <https://doi.org/10.1016/j.applanim.2013.04.011>
- Mellen J and MacPhee MS** 2001 Philosophy of environmental enrichment: past, present, and future. *Zoo Biology* 20: 211-226. <https://doi.org/10.1002/zoo.1021>
- Miller LJ, Pisacane CB and Vicino GA** 2016 Relationship between behavioural diversity and faecal glucocorticoid metabolites: A case study with cheetahs (*Acinonyx jubatus*). *Animal Welfare* 25: 325-329. <https://doi.org/10.7120/09627286.25.3.325>
- Morgan KN, Line SW and Markowitz H** 1998 Zoos, enrichment, and the skeptical observer: the practical value of assessment. In: Shepherdson DJ, Mellen J and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 314-328. Smithsonian Institution Press: Washington DC, USA
- Nakahara F, Komaba M, Sato R, Ikeda H, Komaba K and Kawakubo A** 2017 Spontaneous prosocial choice by captive bottlenose dolphins, *Tursiops truncatus*. *Behavioural Processes* 135: 8-11. <https://doi.org/10.1016/j.beproc.2016.11.009>
- Neto MP, Silveira M and dos Santos ME** 2016 Training bottlenose dolphins to overcome avoidance of environmental enrichment objects in order to stimulate play activities. *Zoo Biology* 35: 1-6. <https://doi.org/10.1002/zoo.21282>
- Newberry RC** 1995 Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* 44: 229-243. [https://doi.org/10.1016/0168-1591\(95\)00616-Z](https://doi.org/10.1016/0168-1591(95)00616-Z)
- Parker RI, Vannest KJ, Davis JL and Sauber SB** 2011 Combining non-overlap and trend for single-case research: Tau-U. *Behavior Therapy* 42: 284-299. <https://doi.org/10.1016/j.beth.2010.08.006>
- Peet RK** 1974 The measurement of species diversity. *Annual Review of Ecology and Systematics* 5: 285-307. <https://doi.org/10.1146/annurev.es.05.110174.001441>
- Perez BC, Mehrkam LR, Foltz AR and Dorey NR** 2018 Effects of enrichment presentation and other factors on behavioural welfare of pantropical spotted dolphin (*Stenella attenuata*). *Journal of Applied Animal Welfare Science* 21: 130-140. <https://doi.org/10.1080/10888705.2017.1383161>
- Puppe B, Ernst K, Schon PC and Manteuffel G** 2007 Cognitive enrichment affects behavioural reactivity in domestic pigs. *Applied Animal Behaviour Science* 105: 75-86. <https://doi.org/10.1016/j.applanim.2006.05.016>
- Samuelson MM, Lauderdale LK, Pulis K, Solangi M, Hoffland T and Lyn H** 2017 Olfactory enrichment in California sea lions (*Zalophus californianus*): An effective tool for captive welfare? *Journal of Applied Animal Welfare Science* 20: 75-85. <https://doi.org/10.1080/10888705.2016.1246362>

- Schneider M, Nogge G and Kolter L** 2014 Implementing unpredictability in feeding enrichment for Malayan sun bears (*Helarctos malayanus*). *Zoo Biology* 33: 54-62. <https://doi.org/10.1002/zoo.21112>
- Serres A and Delfour F** 2017 Environmental changes and anthropogenic factors modulate social play in captive bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology* 36: 99-111. <https://doi.org/10.1002/zoo.21355>
- Shannon CE and Weaver W** 1949 *The Mathematical Theory of Communication*. University of Illinois Press: Urbana, IL, USA
- Shepherdson D, Mellen J and Hutchins M** 2005 *Second Nature: Environmental Enrichment for Captive Animals* pp 172-183. Smithsonian Institution Press: Washington DC, USA
- Shepherdson DJ, Carlstead K, Mellen JD and Seidensticker J** 1993 The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology* 12: 203-216. <https://doi.org/10.1002/zoo.1430120206>
- Similä T and Ugarte F** 1993 Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology* 71: 1494-1499. <https://doi.org/10.1139/z93-210>
- Smith BP and Litchfield CA** 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. <https://doi.org/10.1080/10888700903371863>
- Smolker R, Richards A, Connor R, Mann J and Berggren P** 1997 Sponge carrying by dolphins (*Delphinidae, Tursiops* spp): A foraging specialization involving tool use? *Ethology* 103: 454-465. <https://doi.org/10.1111/j.1439-0310.1997.tb00160.x>
- Swaigood RR and Shepherdson DJ** 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. <https://doi.org/10.1002/zoo.20066>
- Swaigood RR, White AM, Zhou XP, Zhang HM, Zhang GQ, Wei RP, Hare VJ, Tepper EM, and Lindburg DG** 2001 A quantitative assessment of the efficacy of an environmental enrichment program for giant pandas. *Animal Behaviour* 61: 447-457. <https://doi.org/10.1006/anbe.2000.1610>
- Vannest KJ and Ninci J** 2015 Evaluating intervention effects in single-case research designs. *Journal of Counseling and Development* 93: 403-411. <https://doi.org/10.1002/jcad.12038>
- Waples KA and Gales NJ** 2002 Evaluating and minimizing social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology* 21: 5-26. <https://doi.org/10.1002/zoo.10004>
- Wells RS** 2009 Learning from nature: Bottlenose dolphin care and husbandry. *Zoo Biology* 28: 635-651. <https://doi.org/10.1002/zoo.20252>
- White BC, Houser LA, Fuller JA, Taylor S and Elliott JL** 2003 Activity-based exhibition of five mammalian species: Evaluation of behavioral changes. *Zoo Biology* 22: 269-285. <https://doi.org/10.1002/zoo.10085>