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The Frequency of Solitary Behaviors in Captive Odontocetes is Modulated by Environmental and Social Factors

Agathe Serres [1-2], Yujiang Hao [1], and Ding Wang [1]

[1] ***Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China***
[2] ***University of Chinese Academy of Sciences, Beijing, China***

The number of welfare-oriented studies is increasing in captive animals, including odontocetes species that are widely kept in zoos and aquaria. However, validated welfare indicators are lacking for captive odontocetes. We studied the effect of several conditions (time of the day, delay to training, social grouping, public presence, housing pool) and stimuli (enrichment, unusual events) on the solitary behavior of Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*), East Asian finless porpoises (*N. a. sunameri*), and bottlenose dolphins (*Tursiops truncatus*). Each group exhibited different behavioral variations depending on the context. However, some common patterns were found. The frequency of solitary play increased in the 3 groups in positive conditions and decreased in negative contexts. Jumping was mostly displayed in conditions that are thought to be stressful or exciting. Stereotypical behaviors for Yangtze finless porpoises and environment-hitting behaviors for bottlenose dolphins were more frequent during social separation and less frequent when enrichment was provided, suggesting that they could indicate mild stress, lack of stimulation, or frustration. Finally, environmental rubbing seemed to be mostly displayed in quiet contexts. The frequency variation of studied behaviors depending on the context provides preliminary information on their potential use as welfare indicators.

Keywords: bottlenose dolphin, finless porpoise, play, stereotypical behavior, vigilant behavior, welfare

Unlike in Europe or in North America, where the number of facilities holding odontocetes is decreasing (Whale and Dolphin Conservation, 2015), in China, this number is currently increasing (Bossons, 2017; China Cetacean Alliance, 2015, 2019; Vail, 2014). Visitors of such facilities are increasingly sensitive to the animal welfare cause, particularly regarding captive odontocetes. However, the lack of data on their behavior, physiology, or responses to captive management routines (Whale and Dolphin Conservation, 2015) often does not allow for an operative scientific welfare assessment (Brando, Broom, Acasuso Rivero, & Clark, 2017). The Association of Zoos and Aquariums Animal Welfare Committee defines welfare as, “an animal’s collective physical, mental, and emotional states over a period of time, and is measured on a continuum from good to poor” (Association of Zoos and Aquariums, 2016). It is suggested that to assess welfare effectively, multiple parameters including health, physiology, behavior, and cognition need to be measured and combined (Clark et al., 2012; Webster, 2005). Compared with other zoo animals, such as primates, the research about captive odontocetes welfare is scarce (Brando et al., 2017 Clegg, Rödel, Boivin, & Delfour, 2018; Clegg, Van Elk, & Delfour, 2017; Ugaz, Valdez, Romano, & Galindo, 2013). Although the use of a range of welfare indicators is strongly suggested, only few indicators have been studied and validated for odontocetes

Please send correspondence to Agathe Serres (E-mail: agathe.serres11@gmail.com) or Yujiang Hao hao.yj@ihb.ac.cn
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species (Clegg, Borger-Turner, & Eskelinen, 2015; Clegg, Van Elk, & Delfour, 2017; Miller, Mellen, Greer, & Kuczaj, 2011; Serres & Delfour, 2017), and the link between many other parameters and positive or negative welfare states should be tested (Clegg et al., 2015; Brando et al., 2017. Species-specific welfare assessments have to be conducted with validated species-specific welfare indicators (Clegg et al., 2015; Clegg & Delfour, 2018; Mononen et al., 2012; Rushen, 2003). Validation of welfare indicators often implies the measure of different parameters in different contexts, including contexts where animals are likely to be experiencing poor and/or good welfare (Castellote & Fossa, 2006; Désiré, Boissy, & Veissier, 2002).

Because collecting physiological, health, or cognitive data can be challenging as it often requires training and/or complicated protocols, one of the easiest types of data to collect on captive odontocetes, and the most accessible to report upon, is behavior. Behavior is also thought to be a reliable if not the most informative way to measure welfare (Clegg, Van Elk, & Delfour, 2017; Joseph & Antrim, 2010; Maple, 2007). Among all types of behaviors, social behaviors have been the most studied in odontocete species, but solitary behaviors should also be investigated because they could reflect an animal’s emotional state (Clegg & Delfour, 2018). For zoo species, behavioral parameters that are frequently used include stereotypical and other abnormal behaviors (Watters, Margulis, & Atsalis, 2009). In captive odontocetes, described undesired behaviors include circular swimming and high levels of aggressive or sexual behaviors (Clegg et al., 2015; Brando et al., 2017. However, even for these relatively well-studied parameters, few studies statistically analyzed their link with particular living conditions or events that occur in captive facilities to understand their variations and validate them as poor welfare indicators (Clegg, Rödel, et al., 2017). In addition, stereotypical behaviors or abrupt and seemingly abnormal behaviors have never been studied deeper than anecdotal observations in odontocete species (Clegg & Delfour, 2018; Greenwood, 1977; Mason, 1991). Recently, anticipatory behaviors have been investigated to determine the rewarding value of different stimuli for captive bottlenose dolphins (Clegg et al., 2018). Even though these behaviors denote the expectation of a pleasurable event, high levels of anticipatory behaviors are thought to be linked with poor welfare (Galhardo, Appleby, Waran, & Dos Santos, 1996; Spruijt, van den Bos, & Pijlman, 2001; van der Harst & Spruijt, 2007; Watters, 2014), but, because no work has been conducted on odontocete species to confirm this hypothesis, information about these behaviors is lacking. The frustration state that could lead to the expression of abnormal behaviors has been scarcely discussed in studies conducted on odontocetes (Clark, 2013), and many behaviors still need to be understood better (Clegg & Delfour, 2018).

Some behavioral patterns, such as behavioral diversity, exploration, and play, are thought to be potential indicators of welfare for captive dolphins (Galhardo et al., 1996). Play and exploration in mammals were suggested to be indicators of good welfare because they are not observed in conditions associated with poor animal welfare (e.g., lack of resources, extreme temperatures, etc.; Boissy et al., 2007). Play has been extensively studied in captive odontocetes, including locomotor, object, and social play, but few studies investigated its link with welfare (Held & Špinka, 2011, Serres & Delfour, 2017). Many welfare-oriented studies on captive odontocetes focused on enrichment, which aims to increase desirable behaviors (including play) while decreasing undesirable behaviors (Delfour & Beyer, 2012; Eskelinen, Winship, & Borger-Turner, 2015). These studies analyzed the animals' interactions with the provided items or the impact of the presence of enrichment on the animals' behavior, including surfacing events (Maiorano, 2016) or circular swimming (Bahe, 2014). However, many behaviors exhibited by captive odontocetes and the impact enrichment has on their frequency remain poorly studied (Clark, 2013; Eskelinen et al., 2015). In addition, if enrichment is one environmental factor that can impact the animals' welfare, other factors resulting from husbandry practices and/or management of captive groups have been much less studied. Behavioral studies of different species under varying conditions are lacking. Variables that affect the animals' physical, social, or sensorial environment and therefore might cause changes in emotional state and behavior have to be studied more deeply (Clegg, Rödel, et al., 2017).

The most common species of odontocetes found in captive facilities around the world are bottlenose dolphins (*Tursiops truncatus*), belugas (*Delphinapterus leucas*), and killer whales (*Orcinus orca*) (Ceta-Base, 2016; Couquiaud, 2005). They are also the most studied (Hill & Lackups, 2010), including welfare-oriented studies (Clegg & Delfour, 2018). Even though other species are commonly found in aquariums in some parts of the world, such as finless porpoises in Asia (Zhang, Sun, Yao, & Zhang, 2012), studies on their behavior in captivity is very limited, and, to our knowledge, no work has been conducted about their welfare. Because these finless porpoise species are listed as endangered (International Union for Conservation of Nature, 2013), captive individuals are an essential component for better understanding their behavior and conducting captive breeding programs. In order to achieve these goals, the first step is to provide them adequate living conditions and to ensure the animals are experiencing good welfare. However, such objectives cannot be attained without validating indicators to accurately assess these animals' welfare under human care. In this study, we investigated the effect of routine environmental and social factors on the solitary behavior of three groups of odontocetes under human care (Yangtze finless porpoises [YFPs]: *Neophocaena asiaeorientalis asiaeorientalis*; East-Asian finless porpoises [EAFPs]: *N. a. sunameri;* and bottlenose dolphins [BDs]). The aim of this work was to determine if some solitary behaviors were modulated by conditions or events that are thought to impact the animals' welfare state, and therefore if they could potentially be used as welfare indicators for the species we studied.

Method

Subjects, Housing, and Group Composition

Five YFPs were observed in Baiji Dolphinarium, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan (Table 1). When all individuals were housed together, YFPs were kept in a kidney-shaped pool (20 m length × 7 m width × 3.5 m depth), linked by a corridor to a round pool (10 m diameter × 3.5 m depth). These two pools were separated by a gate allowing animals to see each other when separated. A third pool (13 m diameter × 3.2 m depth), not connected to the two others, was used from February 2017 to the end of the data collection to house the female F7 and the male Taotao until F7 gave birth (after birth, she was alone in this pool with her calf, and Taotao was moved back in the two-pool complex).

For group management reasons (i.e., management of pregnant females), the social grouping changed several times during the data collection period (Figure 1). Because the three females gave birth during summer 2018, three calves were also present during certain periods of the data collection (two of them were only present for less than two weeks after their birth, and the third one was present from its birth until the end of the data collection; Figure 1). Four EAFPs and five BDs were observed in Haichang Polar Ocean World, Wuhan (Table 1). EAFPs were always kept together in a rectangular pool (13.75 m length × 8 m width × 5.8 m depth). BDs were kept in a three-pool complex, with two round pools (8.86 m diameter × 5 m depth, "small pools") connected to the main pool (27.44 m length × 12 m wide × 6 m depth, "large pool"). Depending on the observation sessions, animals had access to one, two, or all pools. On January 16, 2017 a new female arrived in the facility, and the other female was placed with her starting January 23. When males and females were separated, females were kept in one of the round pools and males in the other round pool and/or in the main pool. On two occasions, the social grouping changed for a few days (Figure 1). The female Beila was absent from several morning observations because of a medical treatment administered in the medical pool during one month.

YFPs were subject to four to six training sessions per day with no public presentation, but occasional visitors were allowed to watch animals both from the surface and from underwater windows. YFPs were fed between 3 and 3.5 kg of thawed (Basilewsky) and/or live fish per day during training sessions. EAFPs were not trained but had three feeding sessions a day with a total fed of between 2.5 and 3 kg of thawed fish (capelin, herring, squid, mackerel, greasy back shrimp, loach) per day, sometimes including live fish. BDs participated in three training sessions and two public presentations a day (up to five on particular days), within which they were fed between 10 and 13 kg of thawed fish (capelin, herring, squid, mackerel).

Animals were provided human-made objects (i.e., toys) or live fish (for YFPs and EAFPs) at times decided by caretakers, and caretakers frequently interacted with BDs and YFPs outside of training sessions. All pools were frequently cleaned by divers and/or caretakers scrubbing the upper part of the pools' walls.

Table 1

Catalog of Studied Individuals' Features (YFP: Yangtze finless porpoise; EAFP: East-Asian finless porpoise; BD: bottlenose dolphin)

Name	Species	Sex	Age (Year)	Weight (kg)	Length (cm)	Facility
Duoduo	YFP	M	8	NA	157	Baiji Dolphinarium, IHB
F7*	YFP	F	8	NA	145	Baiji Dolphinarium, IHB
F9*	YFP	F	8	NA	145	Baiji Dolphinarium, IHB
Taotao	YFP	M	14	NA	156	Baiji Dolphinarium, IHB
Yangyang*	YFP	F	11	NA	147	Baiji Dolphinarium, IHB
Xiaomeng	EAFP	F	4	33	143	Haichang Wuhan Polar Ocean Park
Xiaomi	EAFP	M	7	31	160	Haichang Wuhan Polar Ocean Park
Xiaoxi	EAFP	M	4	41.5	149	Haichang Wuhan Polar Ocean Park
Xiaozhuang	EAFP	M	7	48	170	Haichang Wuhan Polar Ocean Park
Ailun	BD	M	13	280	274	Haichang Wuhan Polar Ocean Park
Beila	BD	F	11	250	252	Haichang Wuhan Polar Ocean Park
Jiesen	BD	M	14	290	269	Haichang Wuhan Polar Ocean Park
Luoke	BD	M	13	260	270	Haichang Wuhan Polar Ocean Park
R*	BD	F	15	260	255	Haichang Wuhan Polar Ocean Park

Note. *Pregnant females, IHB: Institute of Hydrobiology, Chinese Academy of Sciences

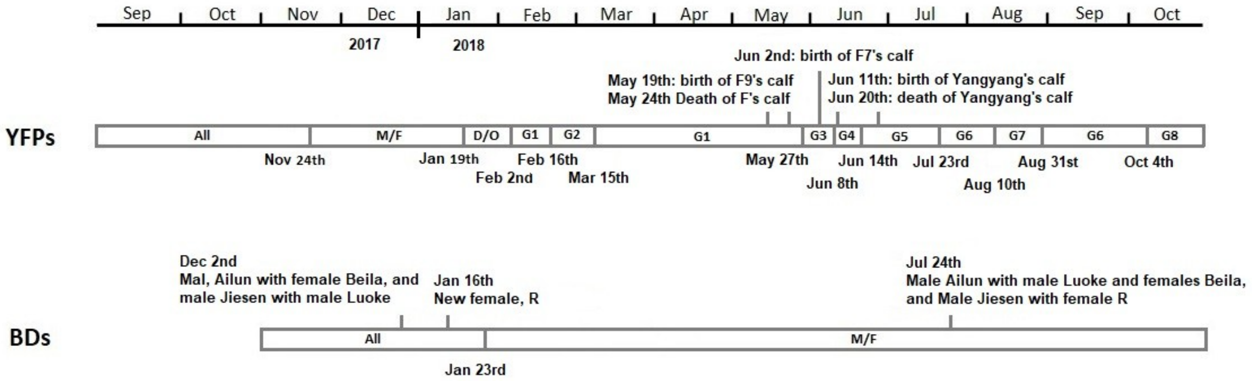

Figure 1. **Social grouping and social events during the observation period for Yangtze finless porpoises and bottlenose dolphins.** All = all animals together; M/F = males and females separated; D/O = Duoduo separated from other YFPs; G1 = Duoduo alone, Yangyang with F9, F7 with Taotao; G2 = Yangyang, F9 and Duoduo together, F7 with Taotao; G3 = Yangyang alone, F9 alone, Duoduo alone, F7 with Taotao; G4 = Yangyang alone, F9 with Duoduo, F7 with Taotao; G5 = Yangyang alone, F7 alone, F9, Duoduo with Taotao; G6: F7 alone, all others together; G7 = F7 alone, Yangyang with Taotao, F9 with Duoduo, G8 = F7 alone, Yangyang with F9, Duoduo with Taotao.

Data Collection

A one-month preliminary *ad libitum* pilot study was conducted to identify and become familiar with each individual and, based on the literature, to build a common ethogram for the three species (Table 2).

The data collection was conducted over 14 months for YFPs and 12 months for EAFPs and BDs. Data were collected two days a week for each group, with no breaks during the data collection period (no week without data collection during the data collection period).

For the formal research protocol, each group was monitored a minimum of three times a day (in early morning, at noon, and in the early afternoon) between training sessions/public presentations/feedings. Observation sessions consisted of 15 min video and voice recordings, using two to six cameras to monitor each group depending on the pool configuration. For YFPs, two underwater and two overhead monitoring cameras were used for the kidney shaped pool, one underwater camera for the connected round pool, and two underwater cameras and one overhead camera for the disconnected round pool. For EAFPs, two Xiaoyi 4K cameras were placed in front of two underwater windows. For BDs, two Xiaoyi 4K cameras were placed in front of a bubble-shaped window, situated 5 m deep in the main pool, and three other Xiaoyi 4K cameras were used to monitor this pool and the other pools from a bridge above. The position of the observation bridge and the small size and depth of round pools enabled the recording of behavior from the surface only. Approximately 90% of every pool was covered by cameras with a satisfactory quality to be analyzed. A complementary direct observation with a voice recorder or with the cameras' audio recording was always conducted synchronously with the video recording to ensure the identification of each individual and to narrate events for easier analysis.

During every data collection day, environmental data were noted. This data consisted of social housing (all animals together: “altogether”, group divided in subgroups: “separated”, individual kept alone: “alone”), pools in which animals were observed (only for BDs, because the pool they were housed in was changing during the day), presence of public, presence of enrichment, and any unusual event that occurred (e.g., pool cleaning; Table 3).

Table 2

Catalog of behaviors and interactions used for the video analysis

Behavior and Description		References
Behavioral Category: Play		
Bubble Play	Any interaction with bubbles emitted by the individual or by another (only observed in YFPs)	Delfour & Aulagnier (1997); McCowan et al. (2000); Xian et al. (2010)
Locomotor Play	Any interaction with the environment or any body movement that occurred repeatedly such as splitting water or beaching (only observed in YFPs and BDs). These behavioral patterns did not always occur at the exact same place in the pool and were not displayed long.	Kuczaj, & Eskelinen. (2014); Xian et al. (2010)
Object Play	Any interaction with an item from the animals' environment such as dirt on the ground of the pool, live fish or toys (bubble play excluded). Depending on the enrichment condition, caretakers could be engaged in object play with animals when toys were provided.	Delfour et al. (2017); Greene et al. (2011); Kuczaj , & Eskelinen (2014); Xian et al. (2010)
Behavioral Category: Other Solitary Behaviors		
Environmental Rubbing	Individual is rubbing a part of its body on the walls or ground of the pool or on the windows	Muller et al. (1998); Xian et al. (2010)
Vigilant Behavior	Individual is looking at the surface, usually in the direction of the place where caretakers typically come from or stand. It could whether look while swimming, stop and look, spy-hop or stay floating in front of the beach while looking (at less than 50cm from the beach, only observed in BDs).	Clegg et al. (2018); Jensen et al. (2013); Xian et al. (2010)
Jump	Individual is jumping or porpoising, with at least 80% of the body coming out of the water	Baker et al. (2017); Holobinko & Waring (2010); Lusseau (2006); Muller et al. (1998); Serres & Delfour (2017); Xian et al. (2010)
Stereotypical Behavior	Individual is engaged in a repetitive behavior with the exact same pattern and at the exact same place for each occurrence (for Xiaozhuang: belly rubbing on the ground in the corner of the pool, for Duoduo	Greenwood (1977); Gygax (1993); Keiper (1969); Mason (1991); Mason & Rushen

	and Taotao: counter-clockwise barrel rolling at a specific point when circular swimming)	(2008)
Environment-Directed Aggression	Individual is hitting a gate or a window with its rostrum or melon (without any human to interact behind the window), or hitting a wall with its peduncle or back, several consecutive times (only observed in BDs).	First described here

Table 3

Environmental and Social Factors' Features (adapted from Serres, Hao & Wang, 2019)

Species	**Time of the day**	**Delay to training**	**Social grouping**	**Unusual events**	**Enrichment**	**Pool**	**Visitors**
YFP	Morning (from 8am to 11:30am)	Away from training	Altogether	None	None	NA	None
	Noon (from 11:30am to 2pm)	Before training (recording ending less than five minutes before the training)	Separated (not alone, gate between groups allowing visual and acoustic contact)	Noise (construction work noise or loud people noise)	Toy(s) (balls)		Few (< 5 persons in front of underwater windows or next to the pool, usually employees or visitors)
	Afternoon (from 2pm to 5pm)		Alone (gate between single individual and others allowing visual and acoustic contact)	Pool cleaning (diver and/or caretaker scrubbing from the surface using long handle brushes)	Human(s) (caretakers interacting with animals outside of training sessions at the surface of from underwater windows, with or without toys)		Many (> 5 persons in front of underwater windows or next to the pool, usually visitors)
				Social unusual event (recording right after separation or reunion of previously seperated groups)			
					Live fish		
				Other event (shoal of small fish in the pool or water level unusually high or low)	New object(s) in the water (Soundtrap, stretcher, experiments' material, new toy)		
EAFPs	Morning (from 8am to 11:00am)	NA	NA	None	None	NA	None
	Noon (from 11:00am to 1pm)			Pool cleaning (diver or small boat)	Toy(s) (balls, Soundtrap)		Few (< 15 visitors in front of underwater windows)
	Afternoon (from 1pm to				Human(s) (public interacting through		Many (> 15 visitors in front of underwater

	4pm)				underwater windows)		windows)
				Noise (construction work, microphone speakers)	New object(s) in the water (Soundtrap, filtration items)		
				Other event (water level unusually high or unknown person sampling water)			
BD	Morning (from 8am to 11:30am)	Away from training	Altogether	None	None	Small (housing pool)	None
	Noon (from 11:30am to 1.45pm)		Separated (gate allowing visual and acoustic contact)	Pool cleaning (divers)	Toy(s) (balls, buoys, ropes with buoys)	Large (public presentation pool)	Few (< 6 persons next to the pool, usually employees)
	Afternoon (from 2pm to 1:45pm)	Before training (recording ending less than five minutes before the training)			Human(s) (caretakers interacting with animals outside of training sessions, with or without toys)	Free access to both large and small	
		During training of other animals (belugas or other group of dolphins when separated)		Noise (public presentation rehearsal or construction work)			
				Social event (separation attempts or introduction of a new individual)			

Note. Training: feeding, training or public presentation

Analysis

Videos were visually analyzed to record all occurrences of previously defined behaviors for each individual using incident sampling (Altmann, 1974; Table 2). All statistical analysis was performed using R 3.6.1.

The effect of environmental parameters (time of the day, delay to training, enrichment, unusual event, separation, presence of visitors, and housing pool; Table 3) on the frequency of each behavior (bubble play, locomotor play, object play, rubbing on the environment, vigilant behavior, jumping, stereotypical behavior, and environment-directed aggression) for each species was analyzed using generalized linear mixed-effects models (GLMMs). GLMMs were conducted using the package “glmmADMB” (Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016) with a negative-binomial family. For each species, one model was run for each behavior. Initially, the behavior frequency as the response variable, the categorical variables time of the day, enrichment, unusual event, separation, public, and pool size were included as predictors; the individual ID, as random factor. For each model, collinearity was tested with variance inflation factor (VIF). Because the variables enrichment and unusual events were often causing collinearity issues when including the different types of enrichment and events, they were transformed into two-level variables (presence/absence). For BDs, the variable delay to training was also transformed into a two-level variable (away from training/before training or while training other animals). Two-level Wald chi-square tests were conducted to extract *p*-values from models. Non-significant variables with a probability value of greater than 0.2 were iteratively removed in a stepwise backward progression and, among reduced models, the one with the lowest Akaike Information Criterion (AIC) was retained. Since EAFPs and BDs were not observed interacting with bubbles, bubble play was only analyzed for YFPs. Locomotor play was not analyzed for EAFPs because we only observed it twice in this group. Stereotypical behaviors were never observed in BDs. We therefore only analyzed it for YFPs (Duoduo and Taotao) and EAFPs (Xiaozhuang). Finally, behaviors that we categorized as environment-directed aggression were only analyzed for BDs since we never observed it in FPs. In this study, we decided to call vigilant behaviors the observation behaviors the animals displayed instead of anticipatory behaviors, as they are called in other studies because of the many contexts in which we conducted our observations. Anticipatory behaviors would imply that animals were always waiting for something, which we think was not always the case (e.g., during unusual events). Because GLMM outputs were on a log scale, means and 95% confidence intervals were back-transformed to be presented in tables and figures.

Results

Data were collected during 142 days for YFPs, 100 days for EAFPs, and 100 days for BDs. In total, every YFP individual was monitored 113 hr (452 recording sessions), 74 hr for EAFPs (297 recording sessions), and 75 hr for BDs (302 recording sessions; Table 4).

Table 4

Catalog of Behaviors and Interactions Used for the Video Analysis

Parameter	Condition	Yangtze Finless Porpoises	East Asian Finless Porpoises	Bottlenose Dolphins
Time of the Day	Morning	166	103	110
	Noon	154	110	109
	Afternoon	132	84	83
Delay to Training	Away from training	438	NA	277
	Before training or training other animals	14	NA	25
Enrichment	No	380	59	226
	Yes	72	238	76
Unusual Event	No	292	237	238
	Yes	160	60	64

Social Grouping	Altogether	130	NA	47
	Separated	304	NA	255
	Alone	18	NA	NA
Visitors	None	333	65	242
	Few	99	189	60
	Many	20	43	NA
Housing Pool	Small	NA	NA	175
	Large	NA	NA	86
	Both	NA	NA	41

Play

Locomotor play differed significantly by time of day for YFPs ($\chi^2 = 6.21$, *df* = 2, $p = 0.04$), with more observed in the morning than afternoon ($\chi^2 = 6.07$, *df* = 1, $p = 0.01$; Table 4). Time of day significantly impacted object play ($\chi^2 = 26.29$, *df* = 2, $p < 0.01$), afternoon produced more object play than morning ($\chi^2 = 20.33$, *df* = 1, $p < 0.01$) and noon ($\chi^2 = 7.35$, *df* = 1, $p = 0.01$). Bubble play revealed no difference for time of day ($p = 0.30$). Bubble play and object play were significantly less frequent right before training than away from it (bubble play: $\chi^2 = 4.89$, *df* = 1, $p = 0.03$; object play: $\chi^2 = 31.41$, *df* = 1, $p < 0.01$). YFPs did not engage significantly more in bubble play, locomotor play, or object play when enrichment was present than when not (locomotor: $p = 0.64$, object: $p = 0.30$. YFPs engaged significantly more in locomotor play ($\chi^2 = 5.51$, *df* = 1, $p = 0.02$) but less in object play ($\chi^2 = 4.85$, *df* = 1, $p = 0.03$) when an unusual event occurred than when not. Bubble play frequency was not significantly impacted by the occurrence of unusual events ($p = 0.81$). When separated, YFPs engaged in significantly more bubble play ($\chi^2 = 9.70$, *df* = 1, $p < 0.01$) and object play ($\chi^2 = 12.23$, *df* = 1, $p < 0.01$) and tended to engage in less locomotor play ($\chi^2 = 3.02$, *df* = 1, $p = 0.08$). The presence of public did not significantly impact the frequency of bubble play, locomotor play, or object play (bubble: $p = 0.91$, locomotor: $p = 0.26$, object: $p = 0.69$.

The frequency of object play was significantly impacted by the time of the day for EAFPs ($\chi^2 = 10.89$, *df* = 2, $p < 0.01$): They engaged significantly less in object play at noon than in the morning ($\chi^2 = 15.22$, *df* = 1, $p < 0.01$) and in the afternoon ($\chi^2 = 9.08$, *df* = 1, $p < 0.01$) and tended to engage in this activity more in the afternoon than in the morning ($\chi^2 = 3.27$, *df* = 1, $p = 0.07$; Table 6). EAFPs engaged in object play significantly more when enrichment was present than when not ($\chi^2 = 134.24$, *df* = 1, $p < 0.01$). The occurrence of unusual events did not significantly impact the frequency of object play in this species ($p = .72$. The presence of visitors tended to impact the frequency of object play in EAFPs ($\chi^2 = 5.05$, *df* = 2, $p = 0.08$), with a significantly lower frequency when many visitors when present than when few visitors were ($\chi^2 = 4.08$, *df* = 1, $p = 0.04$).

Time of day significantly affected locomotor play for BDs ($\chi^2 = 9.74$, $df = 2$, $p = 0.01$), observing more at noon than the morning ($\chi^2 = 6.02$, $df = 1$, $p = 0.01$) and afternoon ($\chi^2 = 8.56$, $df = 1$, $p < 0.01$; Table 6). Object play also differed significantly for time of day ($\chi^2 = 6.42$, $df = 2$, $p = 0.04$), with more in the morning than noon ($\chi^2 = 4.56$, $df = 1$, $p = 0.03$) and afternoon ($\chi^2 = 5.39$, $df = 1$, $p = 0.02$). Object play was significantly more frequent when enrichment was present than when not ($\chi^2 = 252.68$, $df = 1$, $p < 0.01$) and did not vary significantly depending on the delay to training. No significant variation was observed for locomotor play based on the delay to training ($p = 0.94$) or presence of enrichment ($p = 0.34$. Locomotor play decreased significantly during unusual events ($\chi^2 = 11.84$, $df = 1$, $p < 0.01$). Social separation did not significantly impact the frequency of locomotor play ($p = 0.14$) or object play in BDs ($p = 0.33$. BDs tended to engage in locomotor play less when visitors were present than when not ($\chi^2 = 2.78$, $df = 1$, $p = 0.10$). The presence of the public did not significantly impact the frequency of object play in BDs ($p = 0.82$. The housing pool significantly impacted the frequency of locomotor play and object play in BDs (locomotor: $\chi^2 = 81.79$, $df = 2$, $p < 0.01$; object: $\chi^2 = 39.91$, $df = 2$, $p < 0.01$): They engaged in these activities significantly more when housed in the large pool than when housed in the small pool (locomotor: $\chi^2 = 47.13$, $df = 1$, $p < 0.01$; object: $\chi^2 = 13.67$, $df = 1$, $p < 0.01$) or when having access to both pools (locomotor: $\chi^2 = 15.20$, $df = 1$, $p < 0.01$; object: $\chi^2 = 11.77$, $df = 1$, $p < 0.01$), and they tended to engage more in locomotor play when having access to both pools than when housed in the small pool ($\chi^2 = 3.59$, $df = 1$, $p = 0.06$).

Other Solitary Behaviors

The time of the day significantly impacted the frequency of environmental rubbing for YFPs ($\chi^2 = 12.76$, $df = 2$, $p < 0.01$): They displayed it significantly less in the morning than at noon ($\chi^2 = 5.22$, $df = 1$, $p = 0.02$) and in the afternoon ($\chi^2 = 13.99$, $df = 1$, $p < 0.01$; Table 5). The frequency of other behaviors was not significantly impacted by the time of the day (vigilant behaviors: $p = 0.56$, jumping: $p = 0.30$, stereotypical behaviors: $p = 0.65$. YFPs tended to rub less on the environment right before training than away from training ($\chi^2 = 3.83$, $df = 1$, $p = 0.05$). They displayed vigilant behaviors ($\chi^2 = 21.85$, $df = 1$, $p < 0.01$) and jumped ($\chi^2 = 12.99$, $df = 1$, $p < 0.01$) significantly more right before training than away from training. The frequency of other behaviors was not significantly impacted by the delay to training (jumping: $p = 0.38$, stereotypical behaviors: $p = 0.95$). YFPs engaged significantly more in environmental rubbing ($\chi^2 = 13.46$, $df = 1$, $p < 0.01$) but less in vigilant ($\chi^2 = 6.65$, $df = 1$, $p = 0.01$) and stereotypical behaviors ($\chi^2 = 4.72$, $df = 1$, $p = 0.03$) when enrichment was present than when not. The presence of enrichment did not significantly impact the frequency of jumping for this species ($p = 0.24$. YFPs engaged significantly less in environmental rubbing ($\chi^2 = 103.94$, $df = 1$, $p < 0.01$) but jumped more ($\chi^2 = 12.95$, $df = 1$, $p < 0.01$) and were more vigilant ($\chi^2 = 56.84$, $df = 1$, $p < 0.01$) when an unusual event occurred than when not. The frequency of stereotypical behaviors was not significantly impacted by the occurrence of such events ($p= 0.56$). The frequency of jumping was significantly impacted by the social separation condition for YFPs ($\chi^2 = 8.32$, $df = 2$, $p = 0.02$): They jumped significantly more when separated than when altogether ($\chi^2 = 14.34$, $df = 1$, $p < 0.01$) and tended to jump more when separated than alone ($\chi^2 = 3.27$, $df = 1$, $p = 0.07$). The frequency of stereotypical behaviors was also significantly impacted by the social separation condition for YFPs ($\chi^2 = 15.83$, $df = 2$, $p = 0.02$): They displayed it significantly more when separated than when altogether ($\chi^2 = 91.10$, $df = 1$, $p < 0.01$) or alone ($\chi^2 = 15.49$, $df = 1$, $p < 0.01$). The social separation condition did not significantly impact environmental rubbing ($p = 0.31$) and vigilant behaviors' ($p = 0.08$) frequencies. The presence of visitors significantly impacted the frequency of environmental rubbing for YFPs ($\chi^2 = 43.78$, $df = 2$, $p < 0.01$): They displayed it more often when no visitors were present than when few visitors ($\chi^2 = 61.50$, $df = 1$, $p < 0.01$) or many visitors ($\chi^2 = 37.60$, $df = 1$, $p < 0.01$) were present and more when few visitors were present than when many visitors were present ($\chi^2 = 5.23$, $df = 1$, $p = 0.02$). The frequency of other behaviors was not significantly impacted by the presence of visitors (vigilant behaviors: $p = 0.28$, jumping: $p = 0.44$, stereotypical behaviors: $p = 0.58$).

The time of the day significantly impacted the frequency of environmental rubbing for EAFPs ($\chi^2 = 39.44$, $df = 2$, $p = 0.02$): They displayed it significantly more in the morning than at noon ($\chi^2 = 24.57$, $df = 1$, $p < 0.01$) and in the afternoon ($\chi^2 = 22.97$, $df = 1$, $p < 0.01$) and more at noon than in the afternoon ($\chi^2 = 6.72$, $df = 1$, $p = 0.01$; Table 6). The time of the day also significantly impacted the frequency of jumping for EAFPs ($\chi^2 = 9.77$, $df = 2$, $p = 0.01$): They jumped significantly more in the morning ($\chi^2 = 8.61$, $df = 1$, $p < 0.01$) and at noon ($\chi^2 = 4.50$, $df = 1$, $p = 0.03$) than in the afternoon. The frequency of other behaviors was not significantly impacted by the time of the day (vigilant behaviors: $p = 0.53$, stereotypical behaviors: $p = 0.16$). EAFPs displayed significantly more vigilant behaviors when enrichment was present than when not ($\chi^2 = 17.49$, $df = 1$, $p < 0.01$). The frequency of other behaviors was not significantly impacted by the presence of enrichment (environmental rubbing: $p = 0.97$, jumping: $p = 0.17$, stereotypical behaviors: $p = 0.89$). EAFPs jumped significantly more ($\chi^2 = 56.87$, $df = 1$, $p < 0.01$) and engaged in environmental rubbing significantly less ($\chi^2 = 34.13$, $df = 1$, $p < 0.01$) when an unusual event was present than when not. The presence of visitors significantly impacted the frequency of environmental rubbing in this species ($\chi^2 = 24.78$, $df = 2$, $p < 0.01$): It was more frequent when no visitors were present ($\chi^2 = 13.86$, $df = 1$, $p < 0.01$) or when few visitors were present ($\chi^2 = 11.64$, $df = 1$, $p < 0.01$) than when many visitors were present. The frequency of other behaviors was not significantly impacted by the presence of visitors (vigilant behaviors: $p = 0.40$, jumping: $p = 0.87$, stereotypical behaviors: $p = 0.67$).

Table 5

Back-transformed mean frequencies per observation session (15 min), standard-errors, and 95% confidence intervals of recorded behaviors for Yangtze finless porpoises

	Bubble play				Locomotor play				Object play				Environmental rubbing				Vigilant behaviors				Jumping				Stereotypical behaviors			
	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper
Morning	0.17	1.53	0.01	3.42	0.14	1.93	0.00	6.33	0.76	0.81	0.16	3.71	3.40	0.45	1.40	8.28	2.70	0.43	1.17	6.25	0.55	1.99	0.01	27.13	0.03	2.76	0.00	5.60
Noon	0.17	1.60	0.01	3.86	0.08	1.96	0.00	3.83	0.95	0.81	0.19	4.64	4.25	0.46	1.73	10.40	2.92	0.43	1.25	6.81	0.35	1.99	0.01	17.23	0.04	2.77	0.00	8.16
Afternoon	0.24	1.53	0.01	4.83	0.06	1.92	0.00	2.53	1.35	0.79	0.29	6.39	4.53	0.45	1.89	10.89	2.96	0.42	1.30	6.75	0.28	1.90	0.01	11.58	0.03	2.72	0.00	6.56
Before training	0.03	1.34	0.00	0.43	0.01	1.69	0.00	0.38	0.07	0.69	0.02	0.25	2.74	0.40	1.25	6.03	1.01	0.37	0.49	2.08	11.99	1.68	0.45	322.9	0.03	2.40	0.00	3.08
Away from training	0.20	1.55	0.01	4.16	0.10	1.94	0.00	4.38	1.06	0.81	0.22	5.17	4.04	0.45	1.66	9.81	2.95	0.43	1.28	6.80	0.34	1.95	0.01	15.87	0.03	2.76	0.00	6.87
No enrichment	0.21	1.54	0.01	4.20	0.09	1.92	0.00	3.81	0.95	0.80	0.20	4.53	3.77	0.45	1.56	9.10	2.96	0.42	1.29	6.79	0.35	1.93	0.01	15.52	0.03	2.74	0.00	7.42
Enrichment	0.11	1.58	0.01	2.52	0.11	1.97	0.00	5.11	1.10	0.82	0.22	5.49	5.40	0.46	2.20	13.27	2.31	0.44	0.98	5.42	0.64	2.02	0.01	33.27	0.02	2.80	0.00	3.66
No unusual event	0.18	1.53	0.01	3.70	0.07	1.92	0.00	3.05	1.06	0.79	0.22	5.04	5.21	0.45	2.15	12.58	2.32	0.42	1.01	5.31	0.36	1.93	0.01	15.66	0.03	2.74	0.00	6.87
Unusual event	0.20	1.56	0.01	4.20	0.15	1.93	0.00	6.53	0.82	0.81	0.17	4.06	2.46	0.45	1.01	5.97	4.15	0.43	1.79	9.60	0.45	1.98	0.01	21.47	0.03	2.76	0.00	6.19
Altogether	0.37	1.59	0.02	8.53	0.14	1.91	0.00	5.75	0.85	0.80	0.18	4.09	3.62	0.47	1.44	9.15	2.93	0.44	1.25	6.87	0.13	2.29	0.00	11.53	0.00	2.95	0.00	0.52
Separated	0.14	1.60	0.01	3.12	0.08	2.02	0.00	3.95	1.09	0.83	0.21	5.60	4.12	0.47	1.64	10.31	2.77	0.44	1.16	6.58	0.72	2.00	0.01	36.56	0.13	2.79	0.00	3.33
Alone	0.32	1.49	0.02	5.93	0.13	1.87	0.00	4.98	0.37	0.78	0.08	1.73	4.71	0.42	2.05	10.79	3.74	0.41	1.69	8.29	0.03	1.97	0.00	1.441	0.00	2.60	0.00	0.29
No visitors	0.17	1.57	0.01	3.75	0.09	1.96	0.00	4.15	0.95	0.82	0.19	4.71	4.87	0.46	1.96	12.07	2.72	0.44	1.15	6.40	0.36	2.00	0.01	18.09	0.03	2.79	0.00	8.01
Few visitors	0.25	1.66	0.01	6.37	0.08	2.03	0.00	4.45	1.01	0.82	0.20	4.99	2.45	0.47	0.99	6.11	3.21	0.44	1.36	7.53	0.42	2.19	0.01	30.66	0.03	2.80	0.00	6.24
Many visitors	0.22	1.44	0.01	3.78	0.20	1.90	0.00	8.43	1.14	0.77	0.25	5.19	1.64	0.42	0.71	3.77	3.49	0.40	1.59	7.70	1.02	1.92	0.02	44.21	0.01	2.65	0.00	2.66

	Locomotor play	Environmental rubbing	Vigilant behaviors	Jumping	Stereotypical behaviors

	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper
Afternoon	2.84	0.34	1.45	5.53	1.50	0.24	0.93	2.42	0.29	0.32	0.16	0.55	0.00	1.61	0.00	0.05	0.00	3.55	0.00	0.01
Morning	2.35	0.38	1.12	4.96	3.57	0.28	2.07	6.16	0.25	0.39	0.12	0.52	0.03	1.72	0.00	0.91	0.00	2.54	0.00	0.07
Noon	4.21	0.37	2.03	8.74	1.86	0.28	1.09	3.20	0.26	0.37	0.13	0.54	0.02	1.71	0.00	0.46	0.00	2.45	0.00	0.03
No enrichment	0.77	0.34	0.40	1.50	2.19	0.24	1.38	3.47	0.12	0.34	0.06	0.24	0.02	1.52	0.00	0.38	0.00	3.26	0.00	0.04
Enrichment	4.33	0.36	2.13	8.82	2.20	0.26	1.31	3.67	0.32	0.35	0.16	0.64	0.01	1.65	0.00	0.25	0.00	2.62	0.00	0.01
No unusual event	3.05	0.35	1.53	6.06	2.53	0.25	1.55	4.15	0.26	0.34	0.14	0.51	0.01	1.63	0.00	0.14	0.00	2.61	0.00	0.02
Unusual event	3.20	0.38	1.52	6.75	1.24	0.28	0.72	2.16	0.27	0.37	0.13	0.57	0.14	1.60	0.01	3.14	0.00	3.50	0.00	0.02
Many visitors	2.44	0.347	1.26	4.72	1.42	0.23	0.90	2.23	0.23	0.30	0.13	0.42	0.01	1.47	0.00	0.14	0.00	2.88	0.00	0.12
Few visitors	3.16	0.37	1.52	6.55	2.20	0.27	1.29	3.75	0.25	0.37	0.12	0.53	0.01	1.69	0.00	0.33	0.00	2.11	0.00	0.01
No visitors	3.32	0.39	1.54	7.15	2.92	0.29	1.64	5.18	0.32	0.39	0.15	0.69	0.01	1.73	0.00	0.33	0.00	3.24	0.00	0.03

Table 6

Back-transformed mean frequencies per observation session (15 min), standard-errors and 95% confidence intervals of recorded behaviors for East-Asian finless porpoises

The time of the day significantly impacted the frequency of environmental rubbing for BDs ($\chi^2 = 6.55$, $df = 2$, $p = 0.04$): They displayed it significantly more at noon than in the morning ($\chi^2 = 3.87$, $df = 1$, $p = 0.05$) and in the afternoon ($\chi^2 = 7.23$, $df = 1$, $p = 0.01$; Table 7). The time of the day also significantly impacted the frequency of vigilant behaviors for BDs ($\chi^2 = 37.50$, $df = 2$, $p < 0.01$): They displayed it significantly more in the afternoon than in the morning ($\chi^2 = 10.39$, $df = 1$, $p < 0.01$) and at noon ($\chi^2 = 25.86$, $df = 1$, $p < 0.01$) and tended to display it more in the morning than at noon ($\chi^2 = 3.64$, $df = 1$, $p = 0.06$). The time of the day tended to impact the frequency of jumping for BDs ($\chi^2 = 5.86$, $df = 2$, $p = 0.05$): They jumped significantly less at noon than in the morning ($\chi^2 = 904$, $df = 1$, $p < 0.01$) and in the afternoon ($\chi^2 = 5.70$, $df = 1$, $p = 0.02$) and tended to display it more in the morning than at noon ($\chi^2 = 3.64$, $df = 1$, $p = 0.06$). The frequency of environment-directed aggression was not significantly impacted by the time of the day ($p = 0.36$. BDs engaged in environmental rubbing significantly less but in vigilant behaviors and jumping significantly more right before training or when other animals were being trained than when away from training (environmental rubbing: $\chi^2 = 8.89$, $df = 1$, $p < 0.01$; vigilant behaviors: $\chi^2 = 18.31$, $df = 1$, $p < 0.01$; jump: $\chi^2 = 41.97$, $df = 1$, $p < 0.01$). They tended to display more environment-directed aggression right before training or when other animals were being trained than when away from training ($\chi^2 = 3.79$, $df = 1$, $p = 0.05$). BDs displayed significantly less environmental rubbing ($\chi^2 = 6.90$, $df = 1$, $p = 0.01$) and environment-directed aggression ($\chi^2 = 27.50$, $df = 1$, $p < 0.01$) when enrichment was present than when not. The frequency of other behaviors was not significantly impacted by the presence of enrichment (vigilant behaviors: $p = 0.50$, jumping: $p = 0.46$). BDs engaged significantly less in environmental rubbing ($\chi^2 = 18.61$, $df = 1$, $p < 0.01$) and environment-directed aggression ($\chi^2 = 9.63$, $df = 1$, $p < 0.01$) but jumped more ($\chi^2 = 19.47$, $df = 1$, $p < 0.01$) when an unusual event occurred than when not. They tended to display more vigilant behaviors when an unusual event occurred than when not ($\chi^2 = 3.67$, $df = 1$, $p = 0.06$). BDs engaged in environmental rubbing ($\chi^2 = 32.09$, $df = 1$, $p < 0.01$), environment-directed aggression ($\chi^2 = 43.67$, $df = 1$, $p < 0.01$), and displayed more vigilant behaviors ($\chi^2 = 9.53$, $df = 1$, $p < 0.01$) but jumped less ($\chi^2 = 15.25$, $df = 1$, $p < 0.01$) when separated than when altogether. They displayed vigilant behaviors significantly more when visitors were present than when not ($\chi^2 = 10.63$, $df = 1$, $p < 0.01$). The frequency of other behaviors was not significantly impacted by the presence of visitors (environmental rubbing: $p = 0.12$, jumping: $p = 0.92$, environment-directed aggression: $p = 0.37$). The housing pool significantly impacted the frequency of vigilant behaviors for BDs ($\chi^2 = 94.27$, $df = 2$, $p < 0.01$): They displayed it significantly more when housed in the large pool than when having access to both pools ($\chi^2 = 43.12$, $df = 1$, $p < 0.01$) or when housed in the small pool ($\chi^2 = 60.72$, $df = 1$, $p < 0.01$) and tended to display it more when having access to both pools than when housed in the small pool ($\chi^2 = 3.73$, $df = 1$, $p = 0.05$). The housing pool also significantly impacted the frequency of jumping for BDs ($\chi^2 = 13.91$, $df = 2$, $p < 0.01$): They jumped significantly more when having access to both pools than when housed in the small pool ($\chi^2 = 21.89$, $df = 1$, $p < 0.01$) or in the large pool ($\chi^2 = 6.07$, $df = 1$, $p = 0.01$). The housing pool also significantly impacted the frequency of environment-directed aggression for BDs ($\chi^2 = 46.23$, $df = 2$, $p < 0.01$): They engaged in environment-directed aggression significantly less when housed in the small pool than when housed in the large pool ($\chi^2 = 32.46$, $df = 1$, $p < 0.01$) or when having access to both pools ($\chi^2 = 5.05$, $df = 1$, $p = 0.02$) and less when having access to both pools than when housed in the large pool ($\chi^2 = 7.06$, $df = 1$, $p = 0.01$). The frequency of environmental rubbing was not significantly impacted by the housing pool ($p = 0.49$).

Table 7

Back-transformed mean frequencies per observation session (15 min), standard-errors and 95% confidence intervals of recorded behaviors for bottlenose dolphins

	Locomotor play				Object play				Environmental rubbing				Vigilant behaviors				Jumping				Environment-directed aggression			
	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper	M	SE	Lower	Upper
Morning	0.06	0.50	0.01	0.34	0.11	0.50	0.04	0.30	1.52	0.40	0.69	3.35	4.48	0.21	2.99	6.72	2.19	0.42	0.95	5.04	0.48	0.58	0.04	0.37
Noon	0.14	0.60	0.03	0.63	0.06	0.60	0.02	0.21	1.89	0.40	0.87	4.11	3.88	0.21	2.58	5.85	1.32	0.44	0.55	3.17	0.55	0.62	0.19	2.16
Afternoon	0.05	0.53	0.01	0.24	0.07	0.53	0.02	0.19	1.42	0.38	0.67	2.99	5.68	0.19	3.89	8.31	1.88	0.41	0.85	4.18	0.43	0.60	0.13	1.42
Away from training	0.08	0.51	0.02	0.367	0.08	0.51	0.03	0.23	1.68	0.39	0.79	3.59	4.36	0.20	2.96	6.43	1.55	0.41	0.69	3.50	0.47	0.63	0.14	1.64
Before training or training others	0.08	0.71	0.01	0.49	0.05	0.71	0.01	0.21	1.01	0.43	0.44	2.32	6.97	0.22	4.50	10.79	6.63	0.46	2.71	16.25	0.78	0.62	0.16	1.88
No enrichment	0.09	0.54	0.02	0.40	0.03	0.54	0.01	0.08	1.77	0.39	0.83	3.76	4.47	0.20	3.04	6.58	1.81	0.41	0.81	4.03	0.65	0.61	0.20	2.12
Enrichment	0.07	0.47	0.01	0.32	1.57	0.47	0.62	3.95	1.24	0.41	0.56	2.75	4.73	0.21	3.12	7.19	1.60	0.45	0.66	3.85	0.22	0.63	0.06	0.76
No unusual event	0.10	0.52	0.02	0.46	0.08	0.52	0.03	0.23	1.80	0.39	0.84	3.85	4.40	0.20	2.98	6.49	1.51	0.41	0.67	3.41	0.56	0.60	0.17	1.83
Unusual event	0.03	0.55	0.01	0.18	0.06	0.55	0.02	0.19	1.08	0.40	0.49	2.36	5.08	0.21	3.38	7.63	3.02	0.43	1.30	7.03	0.31	0.64	0.09	1.07
Altogether	0.06	0.42	0.01	0.21	0.09	0.42	0.04	0.22	0.74	0.37	0.36	1.52	3.60	0.18	2.52	5.13	3.21	0.38	1.53	6.70	0.12	0.61	0.14	1.55
Separated	0.09	0.54	0.02	0.41	0.08	0.54	0.03	0.22	1.86	0.40	0.86	4.05	4.74	0.20	3.18	7.06	1.57	0.43	0.68	3.61	0.64	0.65	0.22	2.83
No visitors	0.07	0.53	0.02	0.35	0.08	0.53	0.03	0.23	1.68	0.39	0.78	3.65	4.30	0.20	2.88	6.42	1.75	0.43	0.76	4.02	0.51	0.58	0.13	1.32
Few visitors	0.13	0.49	0.03	0.51	0.08	0.49	0.03	0.20	1.36	0.37	0.65	2.84	5.64	0.18	3.94	8.09	1.78	0.39	0.83	3.81	0.42	0.62	0.15	1.72
Small pool	0.04	0.57	0.01	0.20	0.06	0.57	0.02	0.19	1.73	0.40	0.79	3.79	3.63	0.21	2.41	5.49	1.4	0.44	0.60	3.31	0.32	0.60	0.33	3.46
Large pool	0.36	0.49	0.09	1.44	0.16	0.49	0.06	0.41	1.54	0.38	0.73	3.24	7.16	0.19	4.94	10.36	1.92	0.40	0.88	4.22	1.08	0.64	0.17	2.04
Both pools	0.09	0.56	0.02	0.39	0.06	0.56	0.02	0.17	1.34	0.41	0.60	2.99	4.49	0.22	2.94	6.86	3.68	0.44	1.56	8.68	0.58	0.63	0.09	1.10

Discussion

This study showed that the solitary behaviors displayed by the captive odontocetes we observed are modulated by the environmental and social conditions in which they live and the events they experience.

Play

Solitary play patterns exhibited depending on the time of the day were different among the three groups. However, like what was found in previous studies (Delfour & Aulagnier, 1997; Serres & Delfour, 2017), the frequency of most of the solitary play that we analyzed was significantly higher in the morning or at noon than in the afternoon. In addition, play was less frequent right before training than a long time before for YFPs and BDs. This might be due to the anticipation of this event with animals being more attentive to their environment and less likely to engage in other activities (Clegg, Rödel, et al., 2017; Clegg et al., 2018).

The frequency of object play was significantly higher with the presence of enrichment for EAFPs and BDs but not for YFPs. Animals were usually playing with items they were provided (toys, live fish, new objects), which explains the higher frequency of object play. Other types of play were not significantly impacted by the presence of enrichment. We often observed BDs spitting water or loudly whistling when beaching, and we suggest that these behaviors might sometimes be displayed to attract caretakers' attention, but these activities did not appear to be linked with the presence of enrichment. Solitary play is important because, in a human-controlled environment, it allows individuals to exert a control over their own activity (Greene, Melillo-Sweeting, & Dudzinski, 2011). Enrichment has been often studied to determine its effects on captive animals and to find ways to use it efficiently (Delfour & Beyer, 2012; Hoy, Murray, & Tribe, 2010; Kuczaj, Lacinak, & Turner, 1998; Maiorano, 2016; Mason, Clubb, Latham, & Vickery, 2007; Shepherdson, Mellen, & Hutchins, 1998; Shyne, 2006). This tool is widely used in captive odontocetes to increase environmental stimulation and improve animal welfare (Kuczaj et al., 1998; Makecha & Highfill, 2018). To ensure of the efficiency of enrichment, it was suggested that it should be strategically used, monitored, and routinely evaluated (Delfour & Beyer, 2012; Mellen & Macphee, 2001). Here, we did not analyze the reaction of each individual to the presence of enrichment. Different individuals might react differently to enrichment items, and some might reduce unwanted behaviors and increase desirable behaviors for some individuals but not for others (Eskelinen, Winship, & Borger-Turner, 2015; Maiorano, 2016). Therefore, it would be interesting to go deeper in the analysis of each individual's response to each provided enrichment item.

The reaction to unusual events was mixed, with a lower frequency of object play but a higher frequency of locomotor play for YFPs and a lower frequency of locomotor play for BDs. Because play is usually displayed in a relaxed context (i.e., without any threat to the animals; Kuczaj & Eskelinen, 2014), a decrease in play frequency during unusual events is what we expected. This result is also in line with the decrease of social play observed in BDs during noisy construction work (Serres & Delfour, 2017). The increase in locomotor play for YFPs might have been linked with the social events we included in the analysis, which were usually reunion of groups: Following reunions, we often observed animals spitting water.

The separation of animals in several groups significantly impacted YFPs' object play frequency that was the lowest when animals were alone but the highest when separated in several groups. Because toys and other types of enrichment were still provided when separated or alone, the changes in object play frequency resulted from the animals' own choice. Social separation or isolation are thought to be aversive situations (Brunelli & Hofer, 2007; Meyer & Hamel, 2014; Panksepp, 1998, 2005, 2011) and have often been used as stressful conditions during experiments on social animals (horses, *Equus caballus*: Żelazna & Jezierski, 2018; sheeps, *Ovis aries*: Lyons, Price, & Moberg, 1993; dairy calves, *Bos taurus Taurus:* Færevik, Jensen, & Bøe, 2006; for a review, see Hennessy, 1997). Such stressful or uncomfortable situations could therefore have impacted animals' playfulness. When animals were housed altogether, they also had more potential partners with which to interact, and more opportunities to interact, which might have decreased their interest for toys or other items. For YFPs, sociosexual behaviors were particularly frequent between males and females when housed together, whereas when males were separated from females, females rarely interacted with each other. When females were separated from males, they might have played with toys more than when the group was altogether.

Play frequency was not impacted by the public presence for YFPs. Object play decreased for EAFPs and locomotor play increased for BDs with the public presence. It is thought that an individual's reaction to people depends on its species and the individual itself (Hosey, Melfi, & Pankhurst, 2010), which may be an explanation for the differences observed between groups. The decrease observed for EAFPs is in line with previous studies' results stating that the presence of a high number of visitors might be stressful (Chamove, 1988; Cooke & Schillaci, 2007; Fernandez, Tamborski, Pickens, & Timberlake, 2009; Hosey, 2000, 2008; Wells, 2005), and therefore decrease the animals' playfulness. For this species, visitors were constantly present, and animals had no opportunity to withdraw. In addition, high numbers of visitors resulted in a very noisy environment there, whereas for YFPs, visitors were occasional, were told to be very quiet, and were never as many as in the ocean park. For BDs, the public was also occasional and always in low numbers compared with EAFPs, and we often observed BDs beaching, loudly whistling, or spitting water when humans were around, which could be a way for them to attract their attention. In addition, the presence of low numbers of visitors could be a form of enrichment (Baker, 2004; Davey, 2007; Hosey et al.2010; Morgan & Tromborg, 2007), stimulating behavioral diversity and enhancing the animals' playfulness.

For BDs, the frequency of locomotor and object play was higher when housed in the large pool and/or having access to both pools. Having access to a larger space might provide a higher potential for movement to the animals, allowing them to engage in more energetic behaviors. BDs could not engage in beaching play or intense ball play in the small pool for instance. In addition, a previous study showed that cortisol was higher in BDs housed in closed facilities (smaller space) than those housed in open facilities (larger space; Ugaz et al., 2013). The access to a larger space might decrease stress and therefore increase playfulness.

Other Solitary Behaviors

Solitary behavior patterns exhibited depending on the time of the day were different among the three groups. YFPs engaged the least in environmental rubbing but jumped the most. EAFPs engaged the most in environmental rubbing in the morning and jumped the least in the afternoon. BDs engaged the most in environmental rubbing at noon, displayed vigilant behaviors the most in the afternoon, and jumped and displayed vigilant behaviors the least at noon. Only jumping was more frequent in the morning than at noon and in the afternoon for the three groups. Because jumping is often displayed during intense social interactions (e.g., social play, agonistic interactions, Bel'kovich, Ivanova, Kozarovitsky, Novikova, & Kharitonov, 1991; Serres & Delfour, 2017; Trone, Kuczaj, & Solangi, 2005; Würsig & Würsig, 1979, 1980), we suggest that animals might engage in intense social behaviors more often in the morning and might behave more quietly and solitarily during the rest of the day. In addition, YFPs and EAFPs often jumped during pool cleaning, which mostly occurred in the morning. The occurrence of environmental rubbing in the three groups seem to be linked with the periods which were the quietest for the animals. Depending on facilities, animals had different schedules: For YFPs, morning was often more stimulating than noon time or afternoon, with more frequent trainings and routine events, whereas for EAFPs, morning was quieter than noon and afternoon because visitors did not arrive or were present in small numbers. For YFPs and BDs, noon was the quietest moment when caretakers were all leaving; most of the times, only the observer was present. This can also explain the lower frequency of vigilant behaviors at noon for BDs who had nothing to look at at this time of the day.

The frequency of jumping was higher for YFPs and BDs before the training (or when other animals were being trained for BDs) than at other moments. Environmental rubbing and vigilant behaviors were less frequent before the training than away from it for YFPs. The frequency of environment-directed aggression and vigilant behaviors was higher, and the frequency of environmental rubbing was lower before the training (or when other animals were being trained for BDs) than at other moments for BDs. Because training is thought to be perceived as a positive event for animals, in this particular context, we suggest that jumping might be a sign of excitation or frustration. For BDs, this increase in jumping before the training, when other animals were being trained was accompanied by an increase in vigilant behaviors and environment-directed aggression, which is in line with our hypothesis that these contexts could be exciting or frustrating. Because we observed that environmental rubbing was mostly displayed at the quietest times of the day, the lower frequency of environmental rubbing observed for both species might be due to this excitation state and to the activity of caretakers that the animals could see or hear (e.g., preparing fish, training other animals).

The frequency of vigilant behaviors was higher for EAFPs when enrichment was present. In this group, we observed that the presence of objects or humans often resulted in the display of many vigilant behaviors by animals that were not interacting with the object or human (i.e., item monopolized by another individual). Objects (toys) were usually provided in low numbers (one or two items together), and humans were usually either one single trainer or visitors behind underwater windows. Animals who did not have the opportunity to interact with the enrichment (toy or human) might have been seeking another opportunity. Moreover, after caretakers provided toys, animals could have remained vigilant for their trainers, more toys, or a reward. Finally, enrichment provided to EAFPs might have not been suitable. Because we noticed that toys provided were always the same two items and because live fish was provided in small quantities, we think that animals might have habituated to it or played with it for a too short time, and therefore they might have lost their enriching properties. The fact that the decrease of negative behaviors is correlated with the novelty of the enrichment rather than the characteristics of the enrichment supports this hypothesis (Kuczaj et al., 2002; Nash & Chilton, 1986). Oppositely, when enrichment was present, YFPs engaged less in stereotypical behaviors and vigilant behaviors but more in environmental rubbing. For BDs, the frequency of environment-directed aggression and environmental rubbing was lower when enrichment was present. Lack of control over their environment is thought to be one of the causes of the apparition of stereotypical or abnormal behaviors in captive animals (Fraser & Broom, 1990), but many stereotypical behaviors seem to persist over time after their original causes disappeared (Cooper, Odberg, & Nicol, 1996). The effect of enrichment on this kind of behavior has often been studied in terrestrial species (Shyne, 2006), but studies describing captive odontocetes' stereotypical or abnormal behaviors are scarce, and effects of enrichment on these behaviors are still unclear. Because enrichment is supposed to decrease abnormal behaviors (Delfour & Beyer, 2012), the effects we observed on YFPs and BDs' behavior seem to confirm the efficiency of the provided enrichment. Among captive primates, abnormal behaviors include self-hitting, self-biting, and noisy hand clapping (Birkett & Newton- Fisher, 2011). Even though we found no mention in the literature about odontocetes of the wall, window, or gate hitting we analyzed here, BDs have been observed repeatedly pressing their melons against pool walls, which was interpreted as a bad welfare sign (Greenwood, 1977). Abrupt body movements are also thought to be caused by stress in BDs (Frohoff, 1993). The reduction in these kinds of behaviors with the presence of enrichment is thus a positive change. Here, we did not analyze the reaction of each individual to the presence of enrichment. Different individuals might react differently to enrichment items, and some might reduce unwanted behaviors and increase desirable behaviors for some individuals but not for others (Eskelinen et al., 2015; Maiorano, 2016). Therefore, it would be interesting to go deeper in the analysis of each individual's response to each provided enrichment item.

The reaction to unusual events was similar for all three groups with a decrease in the frequency of environmental rubbing and environment-directed aggression for BDs but an increase in vigilant behaviors and jumping. The decrease of environmental rubbing, stereotypical behaviors, and environment-directed aggression might have been caused by the increased vigilant behaviors of the animals as well as their increased swimming speed and social swimming in response to these stressful events (Serres et al., 2019). For instance, animals were frequently looking around during noisy events, including watching the place where caretakers usually stand or come from. The fact that vigilant behaviors increased before the training is congruent with previous studies (Clegg, Rödel, et al., 2017; Jensen, Delfour, & Carter, 2013). Animals were also frequently jumping during unusual events, especially during pool cleaning or separation attempts. The behavioral and physiological reactions of captive animals to different environmental disturbances have been studied, including different kinds of noise, transport events, or human activities (cheetahs, *Acionyx jubatus:* Wells, Terio, Ziccardi, & Munson, 2004*;* giant pandas, *Ailuropoda melanoleuca*: Owen, Swaisgood, Czekala, Steinman, & Lindburg, 2004; bottlenose dolphins: Monreal-Pawlowsky et al., 2017; Serres & Delfour, 2017; belugas, *Delphinapterus leucas*, Castellote & Fossa, 2006; for reviews, see Hosey, 2005; Shepherdson, Carlstead, & Wielebnoski, 2004;).

However, studies on the behavioral reaction of odontocetes to environmental stimuli are scarce and mostly focused on the effect of public presentations or interactions with humans (Kyngdon, Minot, & Stafford, 2003; Miller et al., 2011; Trone et al., 2005). More studies on the animals' reaction to different events are needed to confirm our results.

The separation of animals in several groups had different consequences on YFPs' and BDs' behavior. For YFPs, jumping and stereotypical behaviors were more frequent when separated than when not, although in BDs, jumping was less frequent, but environmental rubbing, vigilant behaviors, and environment-directed aggression were more frequent when separated than when not. For YFPs, we observed animals reacting differently to potentially stressful events when separated and when not: They were often swimming in group during this kind of event when altogether, whereas they were swimming alone and jumping during the same kind of event when separated. This could explain the higher frequency of jumping when separated. Stereotypical behaviors are defined as repetitive and are thought to be displayed in response to an inadequate physical or social environment (Mason, 1991; Mason and Rushen, 2008). The increase of these abnormal behaviors is in line with the fact that social separation or isolation are thought to be aversive situations (Brunelli & Hofer, 2007; Meyer & Hamel, 2014; Panksepp, 1998, 2005, 2011).Animals experiencing social separation have been observed to increase their activity level, as well as stereotypical or abnormal behaviors and contact behaviors for instance (giraffe, *Giraffa camelopardalis tippelskirchi*: Tarou, Bashaw, & Maple, 2000; domestic chicks, *Gallus domesticus*: Rajecki, Suomi, Scott, & Campbell, 1977; dairy cows, *Bos taurus:* Müller & Schrader, 2005; ewes: Poindron, Soto & Romeyer, 1997; ravens, *Corvus corax*: Munteanu, Stocker, Stowe, Massen, & Bugnyar, 2016). The fact that stereotypical behaviors for YFPs and environment-directed aggression for BDs increased when separated reinforces the hypothesis that animals might have lacked social stimulation or might have been stressed or frustrated when separated or alone. Regarding environmental rubbing, odontocetes are known to rub their bodies against various items from their environment (Caldwell & Caldwell, 1972, 1977; Lusseau, 2006), but the purposes of this behavior can be various, including pleasure and masturbation but also skin issues (Brando et al., 2017. Because we observed an increase in environmental rubbing when separated for BDs, we suggest that this behavior might also reflect a lack of stimulation or stress and could become stereotypical. For BDs, vigilant behaviors increased when separated, which reinforces this lack of stimulation hypothesis. Even though separation events occur in facilities keeping odontocetes (Waples and Gales, 2002), the behavioral reaction of animals to separation or isolation was never deeply studied in these species. More research is needed on this point.

For YFPs, the frequency of environmental rubbing decreased with the presence of visitors. This seems to be in line with our previous hypothesis that this behavior could be expressed mostly in a quiet environment with no external stimulations. However, for EAFPs, this frequency increased with the presence of visitors. We often observed the male EAFP, Xiaozhuang, rubbing repeatedly on a wall and thus suggest that this behavior might potentially turn into a stereotypical behavior that could be expressed in response to high public presence for instance. For BDs, the frequency of vigilant behaviors was higher when visitors were present, in line with their higher locomotor play frequency that could be a way to attract humans' attention. Most of the studies investigating the effect of visitors on animals concluded that visitors induce stress (Chamove, Hosey & Schaetzel, 1988; Cooke & Schillaci, 2007; Fernandez et al., 2009; Hosey, 2000, 2008; Wells, 2005), but it is thought that an individual's reaction to people depends on its species and the individual (Hosey et al., 2010). Unlike what we found here, several studies showed that visitors' presence was associated with increased abnormal behaviors, including stereotypical behaviors, self-injuring and aggressive behaviors, and decreased affiliative behaviors (Hosey et al., 2010; Mallapur, Sinha & Waran, 2005). Conversely, few studies suggested that visitors could be a form of enrichment (Baker, 2004; Davey, 2007; Hosey et al., 2010; Morgan & Tromborg, 2007). To our knowledge, the effect of the presence of visitors on captive odontocetes' behavior and welfare has never been conducted. The results we obtained here regarding the public presence are ambiguous, but it might have been caused by our methods: We only used the number of visitors but not their activity level or noise level. In addition, each of our three studied groups was subject to different public conditions, different enclosures, and different kinds of public (for YFPs, visitors were occasionally allowed at the surface and in front of underwater windows, and employees came from the research base; for EAFPs, visitors were always allowed in front of underwater windows; for BDs, aquarium employees were at the surface). All these elements are important biases that might have impacted our data and results (Davey, 2007; Kuhar, 2006). We suggest that more work should be conducted on the influence of visitors on the behavior of odontocetes under human care.

For BDs, being housed in the large pool or having access to both pools increased the frequency of vigilant behaviors, jumping, and environment-directed aggression. The increase of vigilant behaviors when having access to the large pool might be due to the fact that animals were not able to see the training area and could only see a restricted area from the small pool. The fact that jumping was more frequent when having access to a larger space might reflect the higher potential for movement it offers the animals, allowing them to engage in more energetic behaviors. It could also be a sign of positive emotional state or of excitation. However, environment-directed aggression also increased when BDs had access to a larger space. When having access to the large pool, more surfaces on which animals could rub or which they could hit were available, which could explain this pattern. We particularly observed the animals hitting windows that were not present in the small pool, and, instead of two gates in the small pool, they had four they could hit in the large pool. However, if this pattern is due to the higher availability of surfaces, it could also reveal that these rubbing and hitting behaviors were not caused or increased by a small pool size, which goes against the observations of Greenwood (1977), who attributed BDs melon hitting behavior to the small pool size.

The results we found through this study and the patterns we highlighted might be only true for the groups we studied. Because our sample size was small for each species, more work is needed on other groups of the same species and of other species to validate our findings. An aspect that was not studied here and could have resulted in a bias in our results is the effect of contagion in the groups. The activity of an individual might have influenced others who could have engaged in the same activity (play, jumping, etc.; Held & Špinka, 2011; Hill, Dietrich, & Cappiello, 2017; Kuczaj & Eskelinen, 2014). In addition, as we mentioned earlier, even though the behavior was recorded for each individual and we included the individual ID as a random factor in our models, we analyzed the effects of events on the behavior of individuals at a group level; we did not analyze each individual's reaction separately. Because individuals can respond differently to the same stimulus, we suggest that facilities who want to monitor their animals' behavior should do it individually. Moreover, the time of day that observations are conducted has to be taken into account because daily patterns were observed here for each behavior. Finally, the type of enrichment and unusual event effect should be studied more deeply to see which characteristics of these items/events are the most enriching/stressful for the animals in order to improve captive management.

Conclusion

The solitary types of play we studied here increased in frequency in the three groups in conditions that are thought to be positive for the animals and decreased in negative contexts, in line with previous studies' statements. Second, animals mostly displayed jumping in conditions that are thought to be exciting or stressful. This behavior seems to be ambiguous and could be expressed both in pleasurable and exciting contexts (e.g., play, training anticipation) and in stressful situations (e.g., stressful event, social separation). Stereotypical behaviors and behaviors we called environment-directed aggression increased in negative social conditions (separation) but decreased with positive stimuli (enrichment) for YFPs and BDs. Regarding vigilant behaviors, a high frequency could both indicate a lack of stimulation or a state of acute vigilance. Finally, environmental rubbing seems to be mostly displayed in quiet contexts with no external stimulation (e.g., visitors, caretakers' movements). The behaviors we investigated here require to be studied further to confirm the variations we found depending on the context and to validate their potential usefulness in welfare assessment. In order to assess welfare, behavioral data should be used together with physiological and cognitive measures (Clegg et al., 2015; Clegg & Delfour, 2018; Webster, 2005). Measuring welfare is a difficult task, both in captivity and in the wild, and wild and captive animals may not behave or react the same. However, data collected on captive animals brings valuable information about their reactions to environmental stimuli and might be useful for conservation purposes, especially for endangered species such as FPs.

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