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Behavioral patterns are established in response to predictable environmental cues. Animals under human care frequently experience predictable, human-controlled events each day, but very few studies have questioned exactly how behavioral patterns are affected by such activities. Bottlenose dolphins (*Tursiops truncatus*) maintained for public display are good models to study such patterns since they experience multiple daily human-controlled periods (e.g., shows, training for shows, medical training). Thus, we investigated the effect of training session schedule on their “free-time” behavior, studying 29 individuals within 4 groups from 3 European facilities. Our initial time budget analyses revealed that among the behaviors studied, dolphins spent the most time engaged in synchronous swimming, and within this category swam most at slow speeds and in close proximity to each other. “Slow-close” synchronous swimming peaked shortly after training sessions and was low shortly before the next session. Play behavior had significantly higher frequencies in juveniles than in adults, but the effect was only seen during the in-between session period (interval neither shortly before nor after sessions). Anticipatory behavior toward sessions was significantly higher shortly before sessions and lower afterward. We conclude that dolphin behaviors unconnected to the human-controlled periods were modulated by them: slow-close synchronous swimming and age-dependent play, which have important social dimensions and links to welfare. We discuss potential parallels to human-controlled periods in other species, including humans themselves. Our findings could be taken into account when designing welfare assessments, and aid in the provision of enrichment and maintaining effective schedules beneficial to animals themselves.

Keywords: animal welfare, anticipatory behavior, human-controlled periods, play, synchronous swimming

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In humans and nonhuman animals the performance of a behavior might appear arbitrary when viewed discretely, but in general repeatable and identifiable patterns are present across different time-scales. Our knowledge of behavioral patterns in a number of animal species is well-established (Finn et al., 2014; McClintock, Russell, Matthiopoulos, & King, 2013; Stamps, 2016), with notable developments made in circadian and ultradian rhythms (or lack thereof) in general activity and feeding (e.g., Bloch, Barnes, Gerkema, & Helm, 2013; Mistlberger & Skene, 2004; Storch & Weitz, 2009), and aided by new technology (e.g., accelerometers: Robert, White, Renter, & Larson, 2009; Shepard et al., 2008). Behavioral patterns in animals or indeed humans are effectuated in response to the “time-structure” of the surrounding environment (Daan, 1981), where common and predictable salient events entrain the performance of certain behaviors, for example food-searching activity in response to the daily appearance of a food source (Bloch et al., 2013; Storch & Weitz, 2009). Those individuals who use the available environmental cues to structure their behavior around the fulfillment of their needs are considered to be well-adapted to their surroundings (McEwen & Wingfield, 2003; Wingfield, 2005).

Behaviors relating to food acquisition are among the most fundamental to survival, and thus their daily rhythms and “*Zeitgebers*” (entraining stimuli; Aschoff, 1965) have logically been popular research topics for many years. One phenomenon under this umbrella is food-anticipatory activity (FAA), which describes animals’ increased arousal and locomotory behavior before food events that are available on a restricted schedule (Mistlberger, 1994). FAA has been shown to be robust, stable over many daily cycles, and not always within the circadian rhythm (Storch & Weitz, 2009). It has been well-studied in laboratory rodents (see review by Storch & Weitz, 2009) and as result progress has been made into the emotional value of FAA and other types of anticipatory behavior, where it is thought to be a reflection of the “balance of reward systems” experienced by the animal (Spruijt, van den Bos, & Pijlman, 2001). Animals in zoos and aquariums tend to have strongly structured daily schedules of food provision and other events, which are usually highly predictable through numerous environmental cues (Waite & Buchanan-Smith, 2001), promoting the occurrence of anticipatory behavior (Watters, 2014); however, it has not been well-studied in this setting (Anderson, Yngvesson, Boissy, Uvnäs-Moberg, & Lidfors, 2015; Watters, 2014).

Another element of daily behavioral rhythms that has interested researchers is social interaction. Although much less is known about what drives patterns of social behavior (Krause et al., 2013), this topic has recently experienced a surge in interest (see review by Panksepp, Wong, Kennedy, & Lahvis, 2008). Social behavior can be entrained to circadian and ultradian rhythms, and there is also likely to be a prominent genetic influence (Panksepp et al., 2008). Social cues can also be *Zeitgebers* themselves where they stimulate certain patterns of behaviors to occur (Mistlberger & Skene, 2004). Human research has shown that work schedules impact the frequency and type of social behavior conducted in afterwork hours (Ilies et al., 2007; Sonnentag & Bayer, 2005). Investigating animals’ social behavior patterns is not only desirable for its fundamental research value but also in terms of the many applications to management practices (Krause et al., 2013; Mistlberger & Skene, 2004).

Behavioral patterns are more strongly linked to predictable and frequent events occurring in the surroundings, and for animals maintained under human care, the environmental time-structure is largely dictated by human-controlled events or periods of time (Watters, 2014). However, there are only a small number of studies focused on animal behavior in response to human-controlled schedules (Waite & Buchanan-Smith, 2001). Some animals are subject to regular, controlled, nonalimentary events, for example, cows (*Bos taurus*) being milked (Ketelaar-de Lauwere et al., 1999), visitors present in proximity to zoo animals (Hosey, 2005), periods of exercise and being left alone for domestic pets (Lund & Jørgensen, 1999), but nearly all animals are subject to a schedule of food provision by humans. FAA and anticipatory behavior in response to other events is present and increasingly studied in captive animals, particularly in relation to welfare (Anderson et al., 2015; Jensen, Delfour, & Carter, 2013; Spruijt et al., 2001). Very few studies have looked at the variation of social behavior or general activity patterns in response to different management schedules (Storch & Weitz, 2009). However, limited results thus far indicate that as well as food-related behavior, social and other behavioral activity unrelated to human-controlled periods can vary as a result of the time-structure (with primate species: Ulyan et al., 2006; Waite & Buchanan-Smith, 2001).

Bottlenose dolphins (*Tursiops truncatus*) under human care are a striking example of animals that inhabits an environment closely controlled by humans, and their days are generally structured by a number of training sessions. These may constitute shows, show training, medical training, guest interactions, “play” sessions, cognitive tasks (all described hereafter as “training sessions”), but all within which they receive their food as reinforcement after participating in exercises chosen by their care-takers (Brando, 2010). The dolphins and this environment represent a good model for the study of behavioral patterns because they experience repeated and controlled daily events, are easily observable, and are gregarious animals, therefore providing the opportunity to analyze the impact on social behaviors as well. Only a few studies have focused on behavioral patterns in captive dolphins (Galhardo, Appleby, Waran, & Dos Santos, 1996; Nelson & Lien, 1994; Saayman, Tayler, & Bower, 1973; Sekiguchi & Kohshima, 2003), and thus even fewer look at the effect of training sessions. One study found that as the latency to and from sessions varied, the occurrence of dolphins’ behaviors within affiliative, aggressive and repetitive categories also varied, although the authors concluded they were likely *not* caused by the sessions since notable individual behavioral differences were observed (Miller, Mellen, Greer, & Kuczaj, 2011). In addition, anticipatory behaviors were not investigated and one category was used for all social interactions. In a study on three Indo-Pacific humpback dolphins (*Sousa chinensis*) individual differences in behavior were found before and after guest interactions (Sew & Todd, 2013), and thus collective findings were limited. Recently, it was shown that bottlenose dolphins significantly increased the frequency of anticipatory behavior in relation to upcoming training sessions (Jensen et al., 2013). Thus far there have been no findings showing how the daily behavioral pattern of captive dolphins might be structured around the multiple, human-controlled training sessions.

The aim of our study was to investigate how scheduled human-controlled activities modulate animals’ behavior in their “free-time,” through observations of multiple groups of bottlenose dol-

phins in different facilities. Our focus was on behaviors related to the sessions (i.e., anticipatory) and social behaviors. Zoo and aquarium environments promote the development of anticipatory behavior and evidence already supports its presence in bottlenose dolphins (Jensen et al., 2013). We predicted that our defined anticipatory behaviors would increase in the period before the next scheduled session. In a previous similar study, data on synchronous swimming was not taken (Miller et al., 2011), and in another it was chosen to consider any type of swimming as the “default” behavior (Sew & Todd, 2013). As a consequence, a concurrent aim of our study was to investigate, in much more detail than previously, the dolphins’ behavior of swimming synchronously. Other salient social behavior categories (play, aggression, and sexually motivated) were chosen as the most often seen in dolphin interactions (Galhardo et al., 1996; Samuels & Gifford, 1997; Shane, Wells, & Würsig, 1986). Due to the lack of previous studies a priori predictions were not possible, but we expected that at least some social behaviors would vary in relation to the session schedule.

Because daily, human-controlled periods are a common phenomenon for many captive animals, the results of our study could extend to forming cross-species parallels, including behavior of working animals and even regarding the daily routines of humans.

Materials and Method

Study Animals and Facilities

Our study included 29 Atlantic bottlenose dolphins (*Tursiops truncatus*) housed at three European zoological facilities and maintained in four groups, all kept in artificial pool complexes. There were eight dolphins at Parc Astérix (Plailly, France) living in an outdoor pool conjoined to two indoor pools with a total volume of 3,790 m³ of water, where there was always free access to all pools (see Table 1 for age and sex characteristics of the study population). At Planète Sauvage (Port-Saint-Père, France), seven dolphins inhabited four interconnected pools which together contained 7,490 m³ of water. In general the gates to all pools were left open but sometimes access was prevented to pools for maintenance. At the start of the study there were six dolphins in this group but after 2 weeks a 25-year-old female arrived; on her first night she stayed in the medical pool with one other male before being mixed with the group the next day. Dolfinarium Harderwijk (Harderwijk, The Netherlands) housed 14 dolphins in a network of seven pools interconnected by gates and sluice channels, with a total volume of 2,743 m³. The animals at this facility were split

into groups of six and eight animals, where the group of eight participated in the shows while the other six dolphins primarily conducted guest interactions. Of the 29 dolphins in the study population, 25 were captive-born and four originally wild caught. Planète Sauvage and Dolfinarium Harderwijk were open daily to the public for the whole of the study period, and Parc Astérix opened 2 weeks into data collection. At all parks, the dolphins’ diets consisted of a variety of fish and squid species being fed to them at multiple sessions during the day, with the total amount per day for each dolphin ranging between 5 and 12 kg. Also in all parks, during the day there were generally three public presentations (a type of training session but with an audience present) and between two and five other training sessions (which could include training for shows, medical training, play sessions and research sessions), and always having two short feeding-only sessions at the beginning and end of the day. All these types of sessions were considered under the umbrella of “training session” for our methods and analysis, but the potential variance was addressed by testing for effects of type and duration of sessions in our analyses.

Data Collection

Study period. The study took place at all three parks from April 2015 to June 2015, and observations were taken at random times of the day between 07:00 and 21:00.

Behavioral observations. We established a 5-min focal observation protocol with scan sampling every 15s where the behavior being performed was noted down (Martin & Bateson, 1986). Scans where the animal was not visible were recorded so that a percentage of total scans (maximum of 21 scans) could be calculated.

At Parc Astérix, the positioning of underwater windows allowed observations to always be conducted from this location since a large proportion of the pool could be seen at all times, whereas at Planète Sauvage and Dolfinarium Harderwijk the view from underwater windows covered 50% of the pool or less, so observations were conducted above water. Both observation positions were adopted since the pools’ water was always clear, the background color contrasted well with the dolphins’ bodies, and the behaviors were clearly recognizable above and below water. Above and below-water observer positions were at inconspicuous locations to limit the effects on the dolphins’ behavior.

We developed a behavioral repertoire containing 22 behaviors within five categories (synchronous swimming; play; overt aggressive: sexually motivated; anticipatory; see Table A of the supplementary materials), with the aim of including the most common

Table 1
Age and Sex Characteristics of Bottlenose Dolphin Study population

Group	Facility	N total	N females (juvenile/adult)	Age range females	N males (juvenile/adult)	Age range males
1	Parc Astérix	8	0/4	15 to 42	2/2	3 to 33
2	Planète Sauvage*	7	1/2	6 to 25	2/2	4 to 15
3	Dolfinarium Harderwijk	8	—	—	1/7	10 to 41
4	Dolfinarium Harderwijk	6	—	—	2/4	4 to 22

Note. Juveniles: 0 ≤ 10-years-old; Adults: 11-years-old or more.

* One dolphin (female, 25-years-old) joined the group in second week of the observation period.

anticipatory and social behaviors for this species. The behaviors were taken directly or adapted from published repertoires (Clegg, Borger-Turner, & Eskelinen, 2015; Galhardo et al., 1996; Holobinko & Waring, 2010; Samuels & Gifford, 1997). In regard to measuring synchronous swimming behavior, Connor, Smolker, and Bejder (2006) used a differentiation of distance between partners, but here we went a step further and also took into account the speed of the behavior, since it is likely synchronous swimming at different speeds has different functions (e.g., faster in aggressive contexts; Herzing, 1996). Therefore, we defined synchronous swimming by proximity and speed (slow: around 2 m/s or less, minimal tail beats; fast: more than 2m/s and stronger tail beats which may cause head to move up and down; close: contact to partner or within touching distance [≤ 0.5 m]; distant: partner is 0.5 m—one body length away) in order to investigate the variation in each subcategory's occurrence. This yielded four categories of the behavior: slow-close, slow-distant, fast-close, and fast-distant synchronous swimming.

Individual recognition of study animals. No individual tagging or marking was used. Each dolphin could be recognized individually by a combination of: distinct patterns of notches on the dorsal fin and tail, patches of permanent skin discoloration on the body, size and shape of the eyes, and general coloration of the body. It was verified that each observer could identify the dolphins with 100% accuracy, multiple times each, before data collection began.

Observers and interobserver concordance. There were three different observers at each park (IM, MC, and DV), who were all trained by the same person (IC) to use the same data collection techniques and accompanying behavioral repertoire. Prior to the start of data collection an interobserver reliability test was conducted using five randomly chosen video footage samples of 5 min each stemming from different animals. An intraclass correlation based on 1,000 permutations (library *rptR*; Schielzeth & Nakagawa, 2013) revealed a very high concordance in the time budgets of the different behaviors quantified by the three observers with respect to slow-close ($R = .999, p < .001$), slow-distant ($R = 0.992, p < .001$), fast-close ($R = .999, p = .013$), and fast-distant synchronous swimming ($R = .999, p = .012$), and also with respect to sexually motivated behavior ($R = .833, p = .012$) and anticipatory behavior ($R = .904, p < .001$). Play behavior and aggression in these videos was quantified by all observers to be zero, and thus the interobserver agreement was 100% with respect to these behaviors (not tested statistically).

Timing of training. No observations were taken during the training sessions, and the time delay since the last session and until the next one was recorded by the observer for each observation. Subsequently we defined the timing of training variable into three periods: “shortly before:” ≤ 15 min before the next session ($n = 145$ observations); “shortly after:” ≥ 15 min after the last session ($n = 157$ observations); and “in-between:” the intermediate period more than 15 min since the last and before the next session ($n = 724$ observations). It was verified that the data included only observations done when training sessions were at least 30 min apart to ensure these categories were mutually exclusive.

Ethics note. Behavioral observation was the only means of data collection for this study and the ASAB/ABS Guidelines for the Use of Animals in Research (2012) were consulted and followed. As a result of this study all routines remained unchanged

for the animals and the only difference to their environment was an observer standing either by the poolside or at the underwater window for a maximum of 2 hr per day. This study, which was purely observational, was reviewed and accepted by the pluridisciplinary scientific committee of the company representing the facilities.

Data Analysis and Sample Size

Statistical analyses were done with R, version 3.1.1 (R Core Team, 2014). We applied generalized linear mixed-effects models GLMM for proportional data, using a model structure for binomial distribution with a logit link. Calculations were based on Laplacian maximum likelihood estimates using the package *lme4* (Bates, Maechler, & Bolker, 2014); p values were calculated by likelihood ratio tests based on the changes in deviance when a factor was removed from the full main effects model, or an interaction was added to it (Faraway, 2006).

A total of 1,026 5-min observations from 29 different animals (six juvenile males and 16 adult males; one juvenile female and six adult females) from three different facilities and kept in four different groups were available for this study (details on study animals in Table 1). The age class of juveniles included all animals younger than 10 years; older animals were considered as adults (Smolker, Richards, Connor, & Pepper, 1992). All juveniles had stopped nursing at the time of the study. Data were expressed as percentage (for analysis: proportion) of scans (per total visible scans) of the different behaviors, used as dependent variables in our models. Independent variables were the animals' age class, sex (factors with two levels), and the timing of training (factor with three levels), see above for a definition of levels. Due to notable collinearities between sex and age class, these two factors were never tested within the same model. We considered two-way interactions between sex or age class and the timing of training (see Figure 1 for sample sizes within the different levels of the factors).

Models included individual identity as a random factor to account for repeated measurements from the different animals. Overall, we obtained 11 to 57 (on average 35) 5-min observations per dolphin. In addition, we included group identity as a random factor to account for the different origin of the animals and for the dependencies in behavior within groups. We also considered the identity of the facility as an additional random factor which, however, did not account for any additional variation, as it was strongly collinear with the identity of the groups. Thus, this random factor was omitted from the model and these were recalculated. This procedure did not change any of the results obtained. The content of training sessions could vary between free-feeds (no behaviors asked, fish given consecutively until ration is finished), training (rehearsal of known or teaching of new behaviors, husbandry tasks, play or fun sessions) or show/guest interactions (either a show with public present or an interaction session with guests, who remain out of water). As the type of the prior as well as the upcoming session might have potentially and differentially influenced the behavior of the animals, we included “session type” as an additional random factor.

Models were checked for homogeneity of variances and goodness of fit by plotting residuals versus fitted values. As

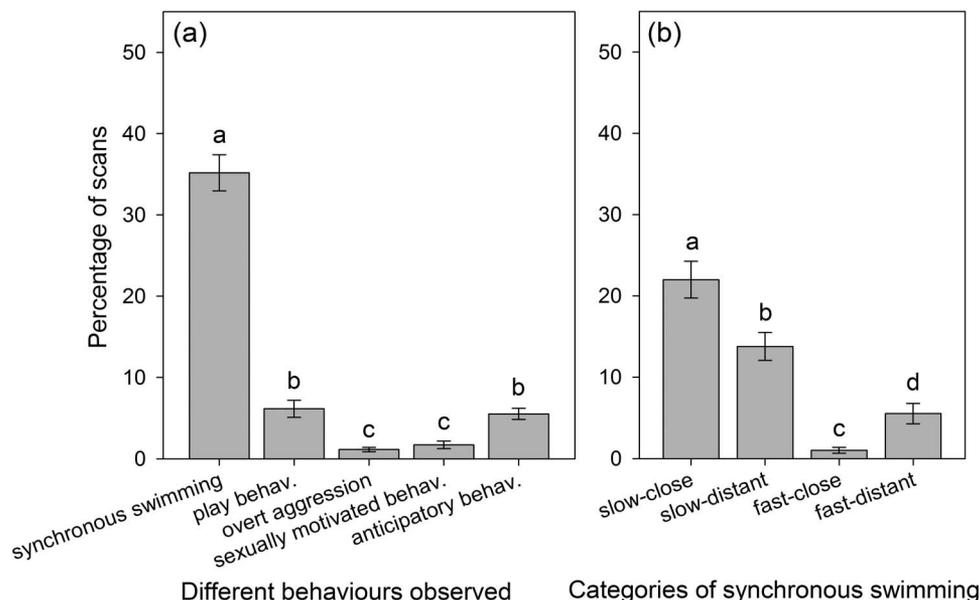


Figure 1. Comparison of different behaviors that bottlenose dolphins displayed during repeated 5-min daylight observations, showing average percentage of scans per 5-min observation spent on (a) the five behavioral categories studied (definitions in Table A); and (b) the four variants of synchronous swimming. Percentage scans denotes the scans where a certain behavior was performed out of the total visible scans in the focal 5 min-observation. Data are based on 1,026 observations from 29 dolphins kept in four different groups. Different letters indicate significant differences between groups, tested by pairwise comparisons using GLMM for proportional data with sequential Bonferroni correction (Holm, 1979).

models showed signs of overdispersion, we included a case-level random factor (Browne, Subramanian, Jones, & Goldstein, 2005). Furthermore, we calculated variance inflation coefficients (VIF) for all models with multiple independent variables (sex and timing of training, or age class and timing of training) to check for (multi)colinearities among them (Zuur, Ieno, & Elphick, 2010). VIF were always lower than 2, indicating no interfering effects of multicollinearities.

Results

Time Budgets of Different Behaviors

The different behaviors observed differed significantly in their occurrence ($\chi^2_4 = 11951.03$, $p < .001$). The behavior which was the most frequent that is, in terms of percentage of scans out of total visible scans per observation (hereafter described as frequency) was synchronous swimming, displayed for an average of 35.2% (CI 95% [33.0%, 37.4%]) of scans per observation (Figure 1a).

Synchronous swimming was categorized into slow-close, slow-distant, fast-close, and fast-distant. These categories also differed significantly in their occurrence ($\chi^2_3 = 115.05$, $p < .001$) with slow-close synchronous swimming displayed most often at an average of 22% of scans per observation, followed by slow-distant at 14%, then fast-distant at 6%, with fast-close swimming occurring in only 1% of observation scans (Figure 1b).

Effects of Different Factors on Behavior

Slow-close synchronous swimming differed significantly with respect to the timing of training (Table 2a). Animals showed significantly lower frequencies of this behavior 15 min before and the highest occurrences 15 min after the training. During the time in-between, that is, between the periods shortly after and shortly before the training, this behavior was seen at intermediate levels (post hoc comparisons in Figure 2a).

Slow-distant synchronous swimming did not significantly differ between the three time periods considered, although the frequencies were significantly higher by 2.0% in males than in females (Table 2b). There were no significant effects of any of the factors considered on the frequencies of fast-close and fast-distant swimming (Table 2c, 2d).

The frequency of play behavior depended on the timing of training session; however, this effect was modulated by the animals' age (see significant interaction in Table 2e). Juveniles showed significantly more play behavior than adults in-between the training sessions, which was on average 2.7 times that of adults. However, differences were not statistically significant during other time periods (post hoc comparisons in Figure 2b).

Anticipatory behavior was seen significantly higher by on average 5.8% of scans per observation shortly before the training sessions when compared to the period shortly after and in-between (Table 2h; post hoc comparisons in Figure 2c).

There were no significant effects of any of the factors tested on the frequencies of overt aggressive or sexually motivated behavior

Table 2
Effects of Sex, Age Class (Juvenile vs. Adult), and the Time Delay to Training (Split Into: ≤ 15 min Before the Session; ≥ 15 min After the Session; and the Period In-Between, i.e. More than 15 min Since the Last and Before the Next) on the Occurrence of Different Behaviors of Bottlenose Dolphins Under Human Care

Response variable	Predictor variable	χ^2	<i>df</i>	<i>p</i>
(a) Synchronous swimming: Slow-close	Sex	.05	1	.82
	Age class	.65	1	.42
	Timing of training	33.82	2	<.001
(b) Synchronous swimming: Slow-distant	Sex	8.45	1	.004
	Age class	2.60	1	.11
	Timing of training	5.42	2	.066
(c) Synchronous swimming: Fast-close	Sex	.13	1	.72
	Age class	.38	1	.54
	Timing of training	1.68	2	.43
(d) Synchronous swimming: Fast-distant	Sex	1.63	1	.20
	Age class	1.73	1	.19
	Timing of training	4.40	2	.11
(e) Play behavior	Sex	1.80	1	.18
	Age class	1.40	1	.24
	Timing of training	.41	2	.82
	Age class \times Timing of training	8.13	2	.017
(f) Overt aggressive behavior	Sex	.89	1	.35
	Age class	2.38	1	.12
	Timing of training	.70	2	.71
(g) Sexually motivated behavior	Sex	1.75	1	.19
	Age class	2.40	1	.12
	Timing of training	.01	2	.99
(h) Anticipatory behavior	Sex	1.75	1	.19
	Age class	.67	1	.41
	Timing of training	9.83	2	.007

Note. Behaviors were measured as percentage of scans out of total visible scans in the 5-min focal observations, and definitions of behaviors in each category are found in Table A. Data stem from 1,026 observations from 29 animals, kept in four groups at three different facilities. Analysis conducted by GLMM for proportional data, including individual identity, group identity, and the type of the previous and following session as random factors. Only statistically significant interactions are given ($p < .05$), and significant differences are highlighted in bold.

(Table 2f and 2g). Additionally, none of the factors or interactions considered were significant when separately analyzing offensive and defensive overt aggression, or acting and receiving sexually motivated behaviors (all $p > .10$).

Discussion

Overall, we found that the schedule of sessions significantly modulated behaviors in the three most commonly shown behavioral categories that we studied: synchronous swimming, play, and anticipatory behavior. Our results showed a peak in slow-close synchronous swimming after sessions, higher frequencies of age-dependent play in the in-between session period, and high levels of anticipatory behavior shortly before training sessions.

Veasey (2006) emphasized how evaluating time budgets of captive animals is fundamental for investigations on how behavioral patterns are affected by management protocols. We used the percentage of scans out of the total visible in 5-min focal observations to formulate a type of time budget, which showed that synchronous swimming was by far the most frequent behavior seen, with play and anticipatory behavior the next most common but relatively at lower levels. This study is the first to separate synchronous swimming by speed as well as

by distance to partner (Connor et al., 2006 defined distances), and the different rates of occurrence indicate that each swimming topography may have a different role in social interactions of dolphins.

Behaviors Modulated by Schedule of Sessions

The frequencies of slow-close synchronous swimming, play, and anticipatory behavior observed in our study were influenced by the timing of sessions. In dolphin species, synchronous swimming has often been suggested as an affiliative behavior which helps to maintain bonds, and is thought to be an indicator of positive emotions (Connor et al., 2006; Holobinko & Waring, 2010). Because the proximity between partners is likely to be salient in relation to the different functions of synchronous swimming (Connor et al., 2006), we chose to study four variants of this behavior and found that only slow-close swimming was modulated with timing to or from sessions. Synchronous swimming in close proximity starts at birth and although the spatial arrangements of the partners develops with age (among other factors), it is thought that dolphins swimming closer together have a stronger relationship (Gubbins, Mcowan, Lynn, Hooper, & Reiss, 1999; Holobinko & Waring, 2010). Therefore, our results of slow-close synchronous swimming is likely to reflect the formation and/or maintenance of

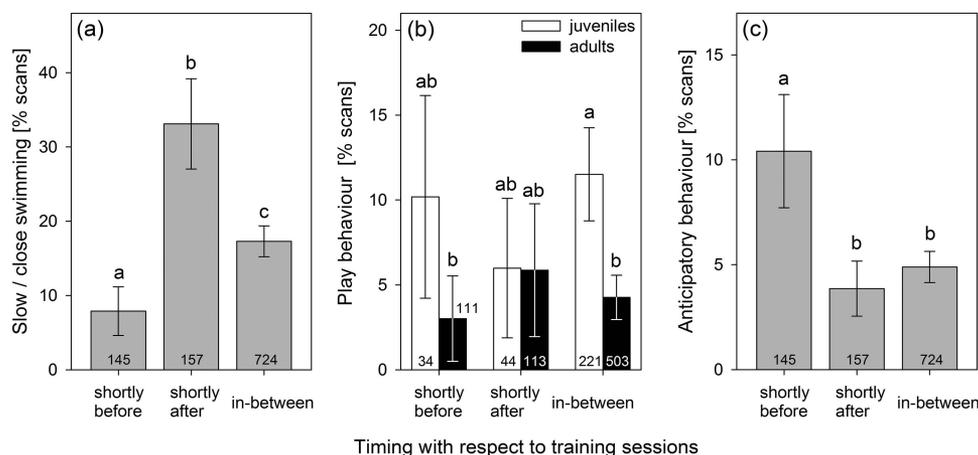


Figure 2. (a) Effects of the timing of training sessions on the percentage of scans per observation of slow-close synchronous swimming, (c) anticipatory behavior, and (b) play behavior where differences were seen between juveniles and adults during the different time periods (significant interaction, see Table 2). Percentage scans denotes the scans where a certain behavior was performed out of the total visible scans in the focal 5-min observation. Sample sizes (total number of observations per group) are given in the bars; see Table 2 for details on statistics. Different letters indicate significant differences between groups, tested by pairwise comparisons using GLMM for proportional data with sequential Bonferroni correction (Holm, 1979).

social bonds in the group, and may be seen more frequently following the sessions because the dolphins are reunited after a human-controlled period of separation. A recent study at Parc Astérix showed that the emission rate of signature whistles increased after the training sessions, and the authors postulated that they function as cohesion calls and affiliative signals: This concurs strongly with the behavioral results in our study (Lopez Marulanda, Adam, & Delfour, 2016). Examples can also be found in other species: Working donkeys (*Equus africanus asinus*) gathered together to socially interact immediately after finishing their working period, even if they were fatigued and dehydrated, and water and food were available (Swann, 2006). Our results with the dolphins' slow-close synchronous swimming concur with the increase in general affiliative behaviors seen after sessions by Miller, Mellen, Greer, and Kuczaj (2011). However, the component of *synchronicity* of this behavior may have a stronger significance than other affiliative behaviors: A recent review concludes that activity synchrony in animals, where behaviors are performed in unison, is itself likely to represent close social bonds between individuals (Duranton & Gaunet, 2016). A recent study found links between the level of synchrony during food provision and milking of cows, to their lying and grazing behavior in their free time (Flury & Gygax, 2016): A similar investigation with dolphins' synchrony during and outside of training sessions might shed further light on this element of their behavior patterns.

An alternative explanation to increased synchronous swimming after sessions might be that it functions as a rest or sleep period. The training sessions are a form of exercise (Brando, 2010), and it is thought that dolphins need to sleep from 4–6 hr per day (range taken from wild and captive research; Goley, 1999; Lilly, 1964; Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008). Their decision to conduct sleep behavior synchronously with others could be an adaptive strategy to improve vigilance (Goley, 1999). However, dolphins perform slow-wave unihemispheric sleep and

thus often do not close both eyes, rendering their sleep behavior “indistinguishable from that of quiet wakefulness” (Oleksenko, Mukhametov, Polyakova, Supin, & Kovalzon, 1992). Therefore, from our results we cannot conclude for certain whether this might have been the true function of the behavior; this might be clarified in further studies.

Play is usually considered an affiliative behavior (Bateson, 2014; Boissy et al., 2007; in dolphins: Kuczaj & Eskelinen, 2014; Neto, Silveria, & Dos Santos, 2016; Paulos, Trone, & Kuczaj, 2010; but see Blois-Heulin et al., 2015; Hausberger, Fureix, Bourjade, Wessel-Robert, & Richard-Yris, 2012) and was performed in our study at higher frequencies in the in-between session period, but only in juveniles. On average there were indications of a similar tendency for shortly before the sessions as well, but this effect was not significant, perhaps due to our smaller sample size of juvenile dolphins. There is evidence that aerial behaviors, a likely component of play, occur more frequently in wild and captive dolphins after a feeding event (Paulos et al., 2010), and it is well-accepted that play occurs mostly when other needs, such as food acquisition, are satisfied (Baldwin & Baldwin, 1976; Bateson, 2014; Boissy et al., 2007). However, while evidence supporting this is available for juveniles in many species, the association between adult play and affective state remains unclear (Blois-Heulin et al., 2015). Our results suggest that juveniles may be more sensitive to the environmental time-structure, leading them to play mostly in the times farthest from the sessions. Alternatively, or in addition, as play is often considered an indicator of positive emotions (Boissy et al., 2007; Held & Špinková, 2011), it could be hypothesized that the juveniles either experience more positive affective states and/or are more aroused/excited in-between the sessions as compared with adults. Further work on the daily patterns of dolphin play with large sample sizes are needed to fully understand this age-dependent element.

The higher occurrence of anticipatory behaviors observed shortly before sessions was the result we most expected to see; a recent first study with bottlenose dolphins found similar results (Jensen et al., 2013) and there is much anecdotal evidence from the animals' care-takers. It was no surprise that dolphins can predict imminent start of training sessions, especially since the timings were fairly regular and environmental cues were available (e.g., sound of buckets) in the three parks in our study. Anticipatory behavior reflects the ability of animals to respond to predictable daily events, but it has also recently been proposed as an indicator of the balance of reward systems (Spruijt et al., 2001). A certain level of anticipatory behavior is thought to reflect positive expectation of the event, but excessive anticipation, either in terms of duration or intensity, may reflect negative affective states such as frustration, perhaps due to lack of other stimulation in the environment (Spruijt et al., 2001; Watters, 2014). Our study provides preliminary results concerning this behavior in dolphins which could then be developed upon in order to investigate certain frequencies relevant to the balance of reward systems.

Our results show that three different dolphin behaviors occurred at predictable points in relation to the session schedule, and that this was not significantly influenced by individual or facility differences. Thus, we might say that these behaviors are entrained in an ultradian rhythm (recurrent cycle repeated within 24 hr) by the timings of the training sessions. Feeding times and rest-activity cycles have been shown to act as *Zeitgebers* as well as light and dark phases (Flury & Gyax, 2016). However, we can only postulate this for our study population due to some limitations which must be discussed. First, much further work would be needed to understand whether it is the food provision or exercise/cognitive element that entrains the rhythm, how easy it is to disrupt, and whether in fact it is social cues that prompt the group to perform a certain behavior in synchrony. Bloch, Barnes, Gerkema, and Helm (2013) recently postulated that highly social animals, and those in a constant environment, are more likely to have ultradian behavioral patterns. Further studies are needed before this can be confirmed for dolphins, where the timings of sessions, environmental cues, and light and dark cycles would need to be controlled for as was not possible in our study.

Relevance to Dolphin Welfare and Implications for Other Species

Overall, our results contribute to improving our knowledge of how the dolphins respond to the captive environment, because an individual's behavioral pattern is a fundamental indicator of how it is adapting to its environment (Eagle & Pentland, 2009; McEwen & Wingfield, 2003; Wingfield, 2005), and thus is highly relevant to evaluating overall welfare (Broom, 1991; Dawkins, 1998; Veasey, 2006). The relatively large sample size of dolphins and observations allowed us to see past short-term individual behavioral differences, which limited conclusions in the previous studies on this topic (Miller et al., 2011; Sew & Todd, 2013; Trone, Kuczaj, & Solangi, 2005). Although not the objective of our study, some possible implications for dolphin welfare and its assessment can be seen in the results.

First, those designing welfare assessments should take into account daily rhythms of behaviors and their likely cues. Here, the dolphin behaviors modulated by the schedule of training sessions

had all previously been suggested as emotion or welfare indicators (Connor et al., 2006; Holobinko & Waring, 2010; Jensen et al., 2013; Neto et al., 2016), and thus in the future might be measured as part of a comprehensive assessment. If this is the case, the timing of human-controlled periods must be taken into account when quantifying such behaviors in dolphins, or indeed other species: The time when a certain welfare measure is conducted in relation to these periods might affect the data collected and conclusions made (e.g., frequency of play behavior).

Our findings also allow us to suggest some more specific implications for dolphin welfare. The performance of synchronous swimming peaked shortly after training sessions and thus in order not to disturb this behavior pattern, it could be beneficial for the management team to not provide environmental enrichment immediately following sessions (as some facilities do) but instead after a short delay. In general, affiliative behaviors (such as synchronous swimming for the dolphins) and juvenile play in animals are thought to be naturally rewarding and induce positive affect in animals (Bateson, 2014; Boissy et al., 2007). Indicators of affective state in dolphin species are highly sought after (Clegg et al., 2015) and we show here that, as well as play behavior, synchronous swimming when delineated by speed and proximity represents a strong potential indicator and deserves further research in this context.

We provide definitions of multiple anticipatory behaviors in dolphins (validated by the significant increase in this activity shortly before sessions), and the fact that this was a concurrent finding despite facility and management differences, for on average 6% of observation time, could provide a starting point for further work on this phenomenon which is thought to indicate welfare state (Spruijt et al., 2001; Watters, 2014). The next step would be to test different frequencies of anticipatory behavior in conjunction with other physiological and cognitive data (Anderson et al., 2015) to investigate whether, and to what extent, it represents either positive affect in the dolphins as they await their "reward" (Spruijt et al., 2001), or whether in some contexts this activity can induce negative emotions such as frustration (Boissy et al., 2007).

There are many other animal species that experience daily human-controlled sessions. Our results correlate to other similar studies: Baldwin and Baldwin (1976) found that feeding ecology and play behavior were closely linked in squirrel monkeys (*Saimia sciureus*) because even changing the form of the food given decreased play behavior significantly, and a few other studies of mammalian species have found that social play increased post-feeding sessions (Cordoni, 2009; Pellis, 1991). The frequency of play and/or affiliative behaviors before or after feeding sessions may be worth investigating as a measure for motivational state of hunger (Pellis, 1991). This could aid management of routines on the commercial scale, for example milking and grazing schedules affecting cow behavior and productivity (Ketelaar-de Lauwere et al., 1999), and would be particularly pertinent as the industry continues to trial automated milking systems (entry and timings under animal control, Flury & Gyax, 2016). Elements of the dolphins' behavioral patterns could also be likened to findings on human routines. For instance Stevenson et al. (1990) used differences in school schedules to highlight the children's need for recess (unstructured free-time) because it gives "opportunities for play," something which we found juvenile dolphins to engage in

specifically in-between controlled sessions. This would suggest that children might also be motivated to interact socially shortly after the lessons end, and therefore planning spaces where children can interact socially and freely in recess times might be beneficial and improve their attention spans (Holmes, Pellegrini, & Schmidt, 2006; Stevenson et al., 1990). Without doubt further research with human subjects is needed to investigate this, especially given that the dolphins' sessions included food provision, but the similarities could be worth considering from both sides.

Conclusions

Through observations of captive bottlenose dolphins we found that slow-close synchronous swimming, age-dependent play, and anticipatory behavior were modulated by the timing of daily human-controlled periods. That social behaviors such as synchronous swimming and play were affected, which would seem to not have as clear, direct connection with the occurrence of training sessions, suggests that the schedule of sessions acts as an entraining cue for the general daily behavioral patterns. We use these preliminary findings to tentatively suggest implications for dolphin welfare, such as the provision of enrichment following a short delay after sessions and the consideration of daily behavioral rhythms when conducting welfare assessments. Furthermore, the three modulated behaviors have all been previously suggested as indicators of dolphin welfare or affective state, but further investigation is needed to discover the actual link between each behavior and welfare and we suggest potential directions to achieve this. Parallels from our findings can be drawn to controlled periods experienced by other species and even humans, providing further evidence that daily schedules are closely linked to behavior in an individual's free-time.

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