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Examining the Relationship between Synchronous Swimming and Partnered Swimming in
Bottlenose Dolphins (*Tursiops Truncatus*)

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Margaret Yuki Kawabata

Committee in charge:

Simone Baumann-Pickering, Chair
Douglas Bartlett
Christine Johnson
David Kacev

2023

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The Thesis of Margaret Yuki Kawabata is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2023

DEDICATION

To my family and all the dolphins in the world.

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ABSTRACT OF THE THESIS

Examining the Relationship between Synchronous Swimming and Partnered Swimming in Bottlenose Dolphins (*Tursiops Truncatus*)

by

Margaret Yuki Kawabata

Master of Science in Marine Biology

University of California San Diego, 2022

Simone Baumann-Pickering, Chair

Synchrony is a well-established behavior that is frequently seen in cetaceans where surfacing events serve as a commonly used marker to spot synchrony due to its visibility from land. However, underwater behavior prior to and followed by synchronous surfacing is limited despite dolphins spending most of their time underwater. Therefore, we report an examination of the relationship between synchronous surfacing and an underwater swimming behavior ‘partnered swimming’ (parallel swimming of dolphins in close-proximity for an extended period of time) based on an observational study of 7 Bottlenose dolphins (*Tursiops truncatus*) kept under human care in Brookfield Zoo, Chicago. Results demonstrated that synchronous surfacing serves as a reliable predictor of partnered swimming

both before and after the surfacing events and further suggest that subjects' preferential associate for the two indices are positively correlated during synchronous swimming in close proximity and aligned orientation. Further results on triadic analysis suggest that proximity in partnered swimming indicates a higher frequency of close-proximity synchronous surfacing between the two that are in closer proximity than the third animal. These results are consistent with previous research on synchrony and proximity and suggest that proximity can indicate the level of synchrony, as evidenced by shorter latency periods between closer-proximal synchronous surfacing events. These findings contribute to our understanding of the social dynamics and affiliative behavior of bottlenose dolphins as surfacing is a social marker to provide a peak in the understanding of a more complex underwater behavior.

INTRODUCTION

Synchrony in Cetaceans

Synchronization occurs when two or more animals perform the same behavior at the same time in close proximity and is a common phenomenon observed in various species of cetaceans (Wursig et al., 1978; Whitehead 1996; Hastie et al., 2003; Connor et al., 2006a). Synchrony is often observed as an affiliative behavior that is essential to maintaining group cohesion in group-living species (Engel & Lamprecht, 1997; Ruckstuhl, 1999) and is hypothesized to be tied to increased foraging success. For instance, bottlenose dolphins (*Tursiops truncatus*) perform synchronous traveling while foraging or feeding (Bel'kovich, 1991), and a similar phenomenon is observed in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) where coordinated hunting efforts were reported to occur with high degrees of synchrony (Saayman et al., 1973). Other fitness advantages are also reported, where synchronous swimming in the form of cohesive schools reduces predation risks (McBride & Hebb, 1948; Norris et al. 1994; Pryor & Shallenberger, 1991), where, for example, Spinner dolphins (*Stenella longirostris*) tend to swim in tighter and more synchronized groups under predation risk (Norris & Dohl, 1980). Fitness advantages to synchrony are reported not only in Delphinidae, but also in the deep-diving Ziphiidae where Aguilar de Soto et al. described Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) to perform precisely synchronized group vocalizations and synchronized diving activity to reduce predation risk by killer whales (2020).

Synchronous Surfacing

Evidence of synchronized behaviors in cetaceans is well-established in numerous studies, where surfacing serves as the most commonly used parameter to measure synchrony due to its observational accessibility from land (Wursig 1978; Heimlich-Boran, 1978; Norris & Dohl, 1980; Jacobsen, 1986;

Whitehead, 1996; Similä & Ugarte, 1993; Perelberg & Schuster, 2008; Actis et al., 2018). Among the various cetacean studies on synchrony, many of them focus on synchronous surfacing in bottlenose dolphins and report various proximate factors, including alliances, body orientation, group size, gender, presence of consortship, presence of calves, and presence of boats (Connor et al., 2006a; Sakai et al., 2010; Connor et al., 2006b; Connor, 2007; McCue et al., 2020; Mann & Smuts, 1999; Hastie et al., 2003).

For instance, Connor et al. (2006a) described synchronized surfacing in male bottlenose dolphins as being correlated with alliance memberships and suggested that participation in synchronization may reflect alliance unity. A similar study also found that both the degree of synchrony and male alliance unity were stronger in inter-alliance groups (two males from the same first-order alliance) than in intra-alliance groups (two members of different first-order alliances) (McCue et al., 2020). Synchronous surfacing is observed not only in males but also in female Indo-Pacific bottlenose dolphins, where females breathe in closer proximity to each other than male pairs (Sakai et al., 2010). Mother-infant relationships are also correlated with synchronous surfacing, where newborn infants synchronously breathe with their mothers more frequently than adults, suggesting a possibility of hydrodynamic advantages for calves to save energy (Mann & Smuts, 1999; Fellner et al., 2006).

The previously mentioned examples were all observational studies on wild Bottlenose dolphins, but synchronous surfacing is also observed in Bottlenose dolphins kept under human care as well. McBride and Hebb (1948) conducted an observational study on dolphins kept under human care and discovered that the rate of synchronous surfacing behavior increased after the introduction of unfamiliar objects into their habitat. Other external objects, like boat traffic, have also been reported to increase the frequency of synchronous surfacing in wild dolphins (Hastie et al., 2003).

Many studies investigating synchrony rely on boat-based focal follows, Unmanned Aerial Vehicles in the field, and telescopic viewing, all of which make observations at the water surface. Such studies are therefore limited, as dolphins spend most of their time underwater, and the behavior observed at the surface only represents a small fraction of their entire social repertoire. To fully understand the implications of synchrony, it is crucial to examine the underwater behaviors before and after surfacing sessions. Thus, the question we ask is, what are bottlenose dolphins doing underwater when we observe synchrony at the surface? What are the implications behind what we see from land? In addition to surfacing, this project will closely examine "Partnered Swimming," where animals swim in close proximity in the same trajectory.

Partnered Swimming

Partnered swimming, as described earlier, is an underwater sustained swimming behavior where two or more animals swim in parallel, following the same trajectory for a fixed amount of time. Evidence of this behavior is commonly reported in a mother-calf pair of bottlenose dolphins (Gubbins et al., 1999), where uniform synchrony is present 90% of the time during the calf's first month in an echelon position, which is a side-by-side position with one dolphin's rostrum no farther behind the other's flukes (Fellner, 2022). As previously stated, hydrodynamic advantages have been discussed as one of the benefits of partnered swimming in different positions such as the echelon position. Partnered swimming is observed not only in mother-calf relationships but also in various other dyadic relationships in odontocetes, where these dyadic relationships have significant implications for high affiliation (Sakai et al., 2010). From the perspective of animal welfare, partnered swimming, which involves synchronous swimming with a partner, is suggested to be linked to odontocetes' emotional state (Clegg, 2017b). Additionally, animals that engage in partnered swimming have been studied to engage more frequently in "gaze-following," an attention behavior where an animal shifts its sensory orientation towards a

particular object or target, followed by an animal that witnessed the shift and also makes the orientation shift (Johnson et al., 2022).

Objective

To understand the implications of synchrony, we will be utilizing subjects that are under human care in their housed habitats, where underwater observations are easily accessible, and sequences of behavior can be carefully analyzed by capturing behaviors in video footage. Therefore, the premise of this study is to investigate the indicative role of synchronous surfacing in partnered swimming behavior, given that we are currently positioned in a manner conducive to such observations from subjects housed at the Brookfield Zoo in Chicago.

In this study, we aim to answer three main questions as follows. First, we ask, for each subject, what is the association between the preferred participant for synchronous surfacing and partnered swimming, and how does the proximity of the synchronous surfacings affect the association index? Next, we will perform a time-series analysis to determine whether synchronous surfacing can predict partnered swimming. In other words, we ask if animals are partnered when synchronous surfacing occurs. Lastly, we investigate whether proximity in partnered swimming affects patterns of synchrony in triads. Here, we will focus on a specific position of triadic partnered swimming called the "AB+C," where two animals (A and B) are close to each other, and the third animal (C) is further away from the two. This triadic position will be further explained in detail in the methods section.

METHODS

Subjects

This study involved seven captive bottlenose dolphins (*Tursiops truncatus*) from Brookfield Zoo in Chicago. The group consisted of three adults aged 24 to 31, three sub-adults aged 9 to 11, and one 7-year-old juvenile. The adult group comprised T (adult female), C (adult male), and A (adult female). T and C had the longest residency, with 14 and 13 years, respectively, while L had the shortest residency at 6 months. T was the mother of N (sub-adult female) and A (juvenile female), both born in captivity. Among the sub-adults, N had the longest residency of 10 years, followed by M (sub-adult male) at 3 years and S (sub-adult female) at 2.5 years. Despite being the youngest, A had a residency time of 10 years as she was born in captivity after her sister N (Table 1). The trainers at the time of the video recording noted that T was the dominant animal in this habitat, and the dolphins associated with others in their age range.

Table 1: Subject animals', age range, sex, kinship -if any, and residency time at the time of the video recording.

Subjects	Age Range/Sex/ Kinship	Residency time at the Time of Video Recording
C	Adult Male	13 years
T	Adult Female (mother)	14 years
L	Adult Female	6 months
M	Sub-adult Male	3 years
N	Sub-adult Female (daughter)	10 years (born in habitat)
S	Sub-adult Female	2.5 years
A	Juvenile (daughter)	7 years (born in habitat)

Setting

The facility in which the subjects were housed had 4 inter-connected habitats, with the main habitat at dimensions of 110' x 40' x 25'. Activities in this habitat were captured with 6 underwater video cameras (black triangles in Figure 1). Animals were able to freely go from one habitat to another whenever the passageways between them were opened; however, all observations for this

study were conducted in the main habitat. This was done between feeding times, when there was no significant human presence. A total of approximately 20 hours of footage were collected over the span of 3 days in February 2014, between 8am and 5pm, using LG Dome Security Digital Video cameras (Model CD14WDR). The 6 views provided almost complete coverage of the main habitat, however, there were some blind spot areas where animals could not be seen, even when present in the main habitat. During data collection for surfacing behavior, animals that had moved temporarily into these blind spots were scored as “unseen”, and so were not included in our analysis. The collected video footage was examined using video player software “ChronoViz”. This program allowed us to view all videos simultaneously, and thus to track all the animals’ movements in the main habitat.

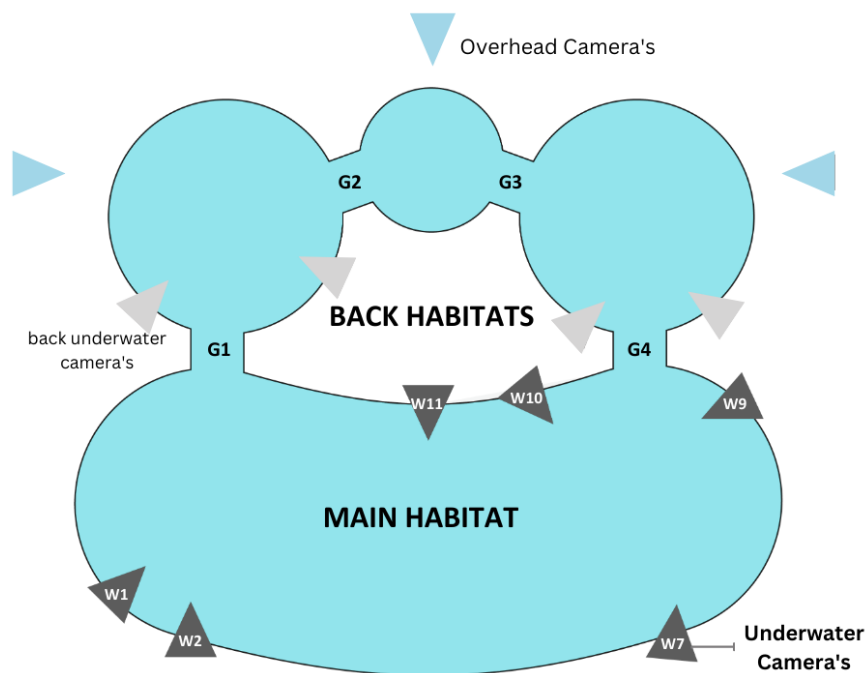


Figure 1: Data Collection was done in the Main Habitat for surfacing behavior. The three circular spaces above make up the Back Habitats. Animals can go in and out of the main habitat to the back habitat using two channels on either end, G1 (left) and G4 (right). The dark triangles are where the six underwater cameras were set to make all observations for surfacing behaviors.

Procedure

This project utilized a combination of three different datasets: Surfacing Behavior Data, Partnered Swimming Data, and Crossings Data. Surfacing Behavior Data were collected specifically for this project, while Partner Swimming Data and Crossings Data were previously collected for other projects. All three datasets were obtained from the same video footage, however, Surfacing Behavior Data were only collected from the main habitat, while Partner Swimming Data and Crossings Data were collected from all 4 inter-connected habitats. Therefore, this project only used data from the main habitat from the three datasets.

Surfacing Behavior Data

To collect Surfacing Behavior Data, scores were recorded for each surfacing event performed by the seven identified dolphins. A surfacing event was defined as an upward projection, followed by the dolphins' rostrums breaking the surface water and an immediate dive. The onset time of the water breakage by the rostrum was used to record the time of the surfacing event. The video footage was collected at a high temporal resolution, with ChronoViz providing data broken down into 10 frames per second. The onset time of the surfacing events was scored down to a half-second interval, where frames between 0 and 4 were rounded down to 0 (e.g., 1.2 seconds was rounded down to 1.0 seconds) and frames between 5 and 9 were rounded to 0.5 seconds (e.g., 1.7 seconds was rounded to 1.5 seconds). If the water breakage was not visible due to the camera angle, the onset time of the water breakage was estimated by subtracting 1.0 second from the dive time. The dive time was identified as the time when the rostrum was at a lower level than the flukes during the downward projection (see Figure 2).

For each surfacing event, the identity of the surfacing dolphin and the identities of any other dolphins present in the main habitat at that time were recorded. If the surfacing dolphin had other

dolphins within a distance of three body lengths (from the tip of the rostrum to the flukes), three body widths (the wingspan from one flipper to the other flipper), and three body depths (from the dorsal fin to the ventral side of the body) surrounding it, those dolphins were recorded as being within the 'social space' of the surfacing animal (see Figure 3). If the animals within the social space were lingering (remaining in the same location for an extended period, either at the surface or underwater), their behavior was recorded, as well as when they were interacting with an object.

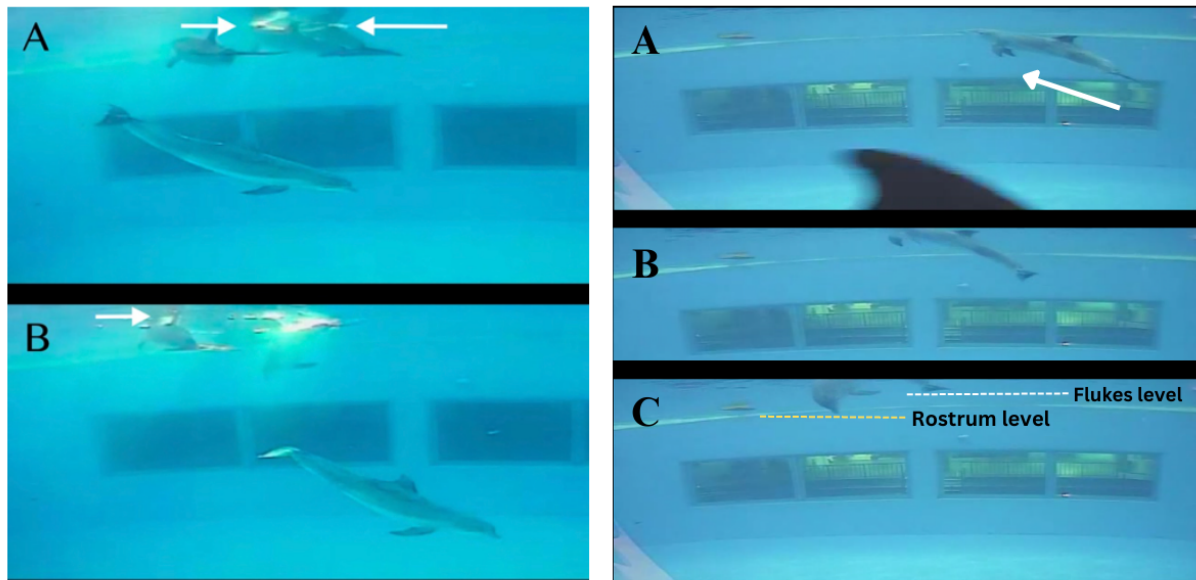


Figure 2: Examples of Surfacing events. The left figure represents when water breakage is seen, indicated by the white arrows. The right figure, shows an upwards projection in panel A, surfacing with uncaptured water breakage due to the camera angle. Panel C shows the dive time of when the rostrum is lower than the flukes.

In the study, there were two different types of surfacing events: Synchronous Surfacing (SS) and Solitary Surfacing. Synchronous surfacing (SS) events were defined as instances when two or more dolphins surfaced with a latency of less than or equal to 2.5 seconds. Three types of SS events were scored: Parallel, Non-parallel, and Far. Parallel SS events were defined when the dolphins participating in the SS event were in close proximity to each other, within each other's "social space", and moving along the same trajectory where "social space" is defined as 3 body widths, 3 body depths, and 3 body lengths from the surfacing animal (see Figure 3). Non-parallel SS events were defined when the synchronous

surfacers were within each other's social space but had different trajectories. Far SS events were defined when the synchronous surfacers were outside of each other's social space. It is important to note that a single dolphin could perform different types of SS events with different dolphins. For example, a focal dolphin could perform a Parallel SS with one dolphin while, at the same time, be synchronous with another surfacing animal farther away as a Far SS event. If an animal surfaced at a time when no other animal surfaced within the 2.5-second window before or after, then the surfacing was scored as "Solitary," indicating that the dolphin surfaced alone.

Partnered Swimming Data

While Surfacing Behavior data were scored second-by-second (with half-a-second precision), Partnered Swimming Data were taken in 10-second intervals. If the partner state changed within the 10-second interval, the interval could be broken down into fourths, making 2.5 seconds the smallest interval to be scored. The main partnered states that were used for this project were "Tight-Partnered Swimming", "Loose-Partnered Swimming", and "non-Partnered Swimming". Tight-Partnered Swimming was when 2 or more animals swam with the same trajectory, where the distance between them was a maximum of 1 body width, and, length-wise, at least some portion of their two bodies overlapped (See Figure 3). Loose-Partnered Swimming was when 2 or more animals swam with the same trajectory, but within a maximum of one body length between the animals, in any direction (see Figure 3). Non-Partnered Swimming involved the animals at any distance, and any trajectory, outside the above-specified limits.

Partnered State was collected from every animal's focal perspective. Thus, there were seven different datasets of Partnered Swimming Data, one for each animal. A focal animal can simultaneously have both Tight and Loose Swimming Partners, but it is important to note that a particular partner

cannot be counted as both Tight and Loose, as these categories are mutually exclusive. For instance, a focal animal A can have a partner B who is Tight, and partner C who is Loose with both A and B. This particular formation is called an “AB+C” formation and will be closely examined when studying triads.

Crossings Data

Another previously collected dataset named "Crossings" was also used in this project. The Crossings data consisted of second-by-second scoring, indicating which habitat or channels each dolphin was present in at a given time. Like all other data used in this project, the Crossings Data were taken from the same video footage of the habitat in Brookfield Zoo. In the Surfacing's study, the Crossing data were used to determine which animal was present in the main habitat at the time of any surfacing event.

Control and Consensus in preparation for Data Collection

While ChronoViz calibrated the data to play videos simultaneously, manual calibrations needed to be performed due to the video cameras having different frame capture rates: some cameras captured 10 frames per second, while others captured more than 10 frames per second. Since the premise of the project was to examine synchronous behavior, which relied heavily on accuracy and precision in time, detailed inspections were performed to ensure that videos were playing simultaneously by identifying overlapping animals between the cameras and checking the animals' body movement frame by frame.

For the SS data, seven observers were trained over the course of 6 months to accurately identify all seven animals using the six underwater cameras in the main habitat with the software ChronoViz. To control the reproducibility of the data, an inter-rater reliability, using Cohen's kappa coefficient (k), was used to measure the agreement in data collection among the seven observers. A coefficient value of $k=1$

represents complete agreement among the raters, while $k=0$ indicates no agreement other than what is expected by chance. The seven trained observers had coefficient values of >0.9 before collecting surfacing data.

Data Control and Statistical Analysis

After combining the three datasets, we conducted sequential analyses to enable time-series analysis. However, before proceeding, two factors were examined to assess variability based on the subjects' tendencies: surfacing rate and presence time. In particular, the previously collected data showed significant variability in presence time. To investigate if any subjects were under-represented based on the interquartile range (IQR) of their presence time, we employed Tukey's range test. The IQR was calculated using the equation:

$$IQR = Q3 - Q1,$$

where Q3 represents the third quartile (75% of the entire dataset range) and Q1 represents the first quartile (25% of the entire dataset range). Tukey's method assesses the spread of data between the quantiles and identifies outliers as any data point that lies more than 1.5 times the IQR above the upper bound ($Q3 + 1.5 * IQR$) or below the lower bound ($Q1 - 1.5 * IQR$). We utilized Tukey's method to investigate any outliers in both surfacing rate and the percentage of partnered swimming within the subjects.

The seven subjects had varying durations of presence in the main habitat. To control for each animal's time spent in the main habitat, which was calculated from the crossings data, we utilized it as a factor in investigating dyadic surfacing behavior and dyadic partnered swimming behavior. The following calculations were employed:

$$\text{Dyadic Surfacing Rate} = \frac{\text{Frequency of dyad's surfacing events}}{\text{Co-Presence Time in main habitat}}$$

$$\text{Dyadic \% Partnered Swimming} = \frac{\text{Partnered Swimming Duration}}{\text{Co-Presence Time in main habitat}} \times 100\%$$

Since there were four different types of surfacing events (Parallel SS, Non-parallel SS, Far SS, and Solitary Surfacing), corresponding surfacing rates were calculated for each type.

All statistical analysis were be performed using the free software R (version 4.3.0). Pearson's Correlation Test was be used to investigate the relationship between SS preference and partnered swimming preference per animal. Pearson's correlation test operates under the assumption that the data to be used are intervals or ratios, that both variables follow normal distributions, there are no outliers, and that linearity exists between the two variables, all of which were tested prior to performing Person's Correlation Test. Furthermore, before conducting Pearson's Correlation Test, the variable % partnered swimming underwent an arcsin transformation,

$$\text{Transformed \% Partnered Swimming} = \arcsin \left(\sqrt{\left(\frac{\% \text{ Partnered Swimming}}{100} \right)} \right)$$

since values for percentages are bound from 0 to 100 whereas the comparator variable, rate of SS, were not bound.

In addition to the correlation test, a chi-square test was employed to examine the association between dyad's SS rate and % partnered swimming. The null hypothesis assumed no association between SS rate and % partnered swimming. Specifically, the total frequencies of surfaces were examined for four different categories: SS during Partnered-Swimming, SS during non-Partnered-Swimming, Solitary Surfacing during Partnered-Swimming, and Solitary Surfacing during non-Partnered Swimming.

RESULTS

Descriptive Analysis of Patterns of Surfacing

A total of approximately 17 hours of video footage were reviewed to collect observational data. From the video footage, a total of 6,951 surfacings were observed where 3,321 surfaces were SS, and 2715 were solitary surfaces and 915 were surfaces in chains where individual surfacing frequency and their corresponding surfacing rates are shown in Table 2.

Table 2: Summary of Surfacing Data per subject. The ID represents each dolphin, A, C, L, M, N, S, and T. The Pres. Time represents each animal's total time present in the main habitat. Frequencies are shown under the Solitary Surfacing column, Synchronous Surfacing column, Parallel SS, non-Parallel SS column, and Far SS column.

ID	Pres. Time (sec)	Solitary Surfacing	Synchronous Surfacing (SS)	-----Types of SS -----		
				Para	non-Para	Far
A	49545	317	321	132	33	156
C	52849	511	449	170	35	244
L	48797	342	412	189	23	200
M	36675	277	366	197	17	152
N	38077	324	361	206	16	139
S	14084	160	257	123	21	113
T	52272	215	698	443	42	213

Now, shown in Figure 4, surfacing rates amongst each subject were consistent at an average of 86 surfaces/hour with a standard deviation of 6.17 surfaces per hour. While surfacing rates included surfaces that happened in chains, further analysis omitted chain events due to the complexity of chain events since they cannot be compared to standard SS events where all members in the scene are synchronous with one another.

Additionally, 164 surfacing events were omitted because the surfaces had other animals in their “Social Space” that were not fully captured by the camera. 431 surfacing events contained lingering animals and 493 surfacing events contained animals in their social space that interacted with objects. Sincere these events were observations of “distracted” animals, they were also omitted for further analysis. Of the remaining 2,864 SS's, 1,460 contained Parallel SS, 187 contained non-Parallel SS, and 1,217 contained Far SS (see Table). The average latency of SS was 1.86 seconds, where Parallel had the smallest latency of 1.69 seconds, non-Parallel had a latency of 2.32 seconds, and Far had a latency of 2.33 seconds. The total duration of all triadic partnered swimming was 16272.5 seconds, which was approximately 4.5 hours as opposed to dyadic partnered swimming of 21287.5 seconds or 5.9 hours.

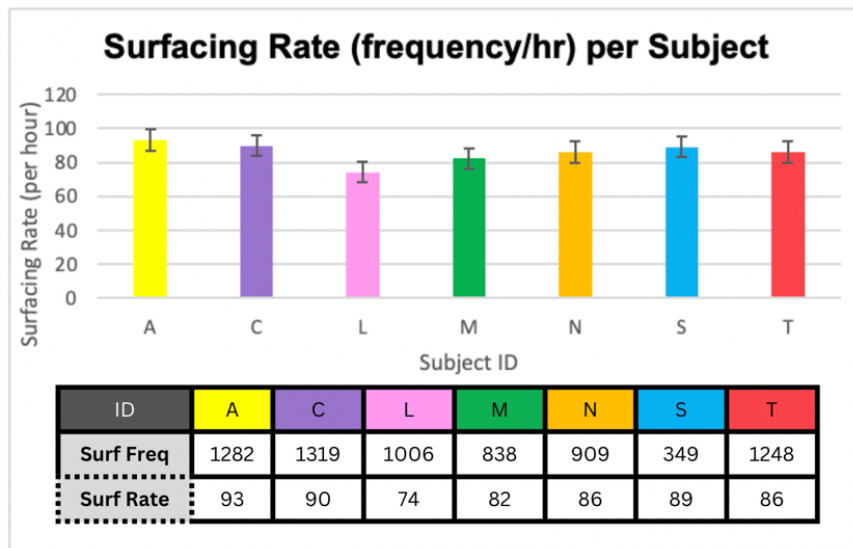


Figure 3: Bar plot of Surfacing Rates in frequency/ hour, as well as a table of surfacing frequency and surfacing rate below.

Crossings Data: Two main Groups ACLT and MN

According to the crossing data, the average presence time in the main habitat was 41,757 seconds, approximately 11.6 hours among the seven subjects. However, animal S had a significantly lower presence time, accounting for only about a third of the average, at 14,084 seconds or 3.9 hours.

To investigate if S's lower representation is due to its shorter presence time, Tukey's range test was conducted. It revealed that S's presence time was 0.89 hours lower than the lower bound of 4.775 hours. When examining the percentage of co-presence relative to the individual presence ($\% \text{ Co-presence} = \text{Co-Present Duration} / \text{Individual Total Duration}$), animals showed a tendency to spend their time in two distinct cohorts, ACLT and MN, with S being an outlier as mentioned before. Specifically, S spent 93.6% of her time with the MNS group. However, this was not reciprocated by animals M and N, as they spent over 93.8% of their time together without S, and only spent 35% of their time together with S. It is important to mention that the discussed cohort only includes sub-adults. Moving on to the ACLT cohort, which consisted of all adults and a juvenile daughter, all four members spent more than 78.0% of their time co-present with each other. The low presence time of S shows an under-representation of S, evident in the lack of reciprocity of co-presence within the sub-adults. Thus, S was removed upon further analysis.

Partnered Swimming

For the analysis of partnered swimming behavior, the same 69,489 seconds (approximately 19.3 hours) of the video footage used for surfacing data were utilized. Fifteen dyadic relationships were evaluated among the six animals (A, C, L, M, N, and T). The % Loose Partner-Swimming and % Tight Partner-Swimming for each dyad are summarized in Appendix A, along with the co-present duration derived from the Crossings Data, arranged in descending order based on the % Loose Partner-Swimming. The results were consistent with the findings from the Crossings Data, indicating that animals engaged in partnered swimming with members of their cohort.

By combining the data collected for surfacing behavior and partnered swimming, we can now proceed with the analysis of the three objectives of this project: 1) Association between preferred

partner for the three types of SS and Partnered-Swimming, 2) Assessing the partnered state during a surfacing, and 3) Investigating triadic surfacing patterns during an AB+C formation.

Q1: Association between preferred associate for SS and Partnered-Swimming

To examine the association between the preferred associate between different types of SS and Partnered Swimming, a Pearson's Correlation Test was conducted for each of the six focal animals when paired with one another in dyads. The test examined the relationship between % Partnered Swimming and the three types of synchronous surfaces: Parallel SS, non-Parallel SS, and Far SS where results are summarized in Figure 4.

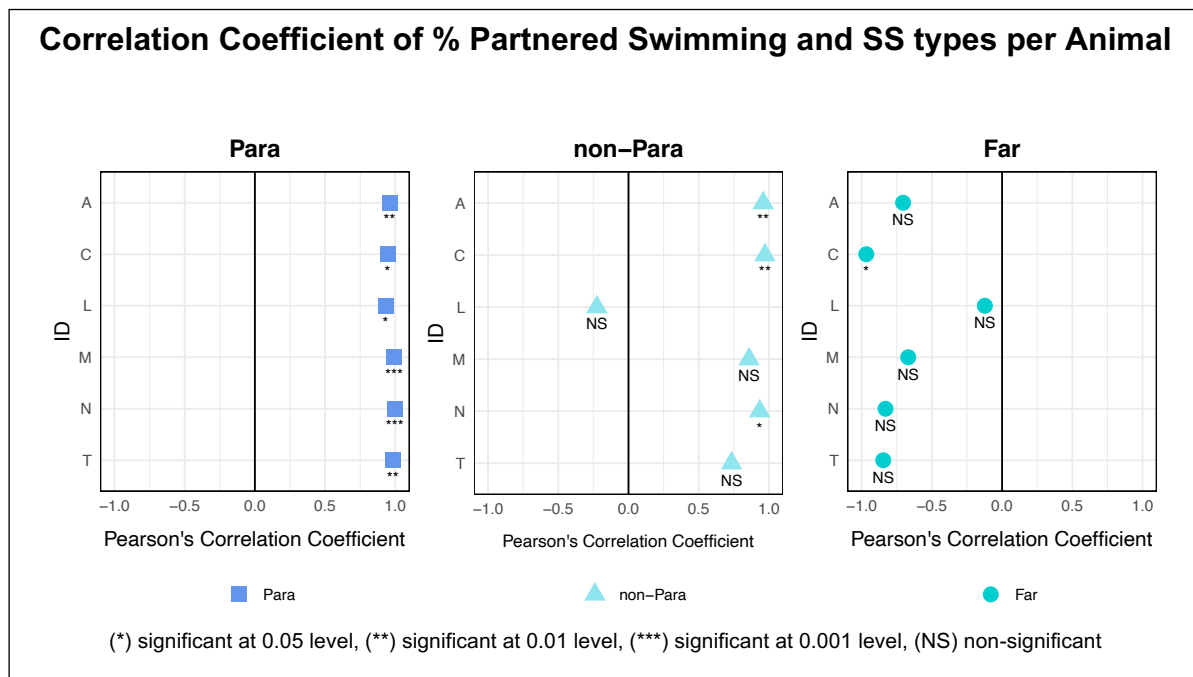


Figure 4: Pearson's Correlation Coefficient for Partnered Swimming associate and three types of SS associates, Parallel SS/ non-Parallel SS/ Far SS from left to right. The x-axis represents the correlation coefficient values, indicating the strength and direction of the correlation, while the y-axis represents the results for each subject.

Parallel SS and Partnered Swimming: For all six animals, the rate of Parallel SS and %Partnered Swimming showed a positive correlation at an average Pearson's Correlation Coefficient (r) of 0.9678 that were all significant at the 0.05 level. Of all six, M and N, who had the highest level of correlation of $r = 0.9916$ and $r = 0.9834$ respectively, had the highest levels of significance at the 0.001 level.

Non-Parallel SS and Partnered Swimming: Association between non-Parallel SS and % Partnered Swimming, was not as strong nor significant as Parallel SS, where half of the subjects had results that were non-significant. A, C, and N all showed strong positive correlations at an average of $r = 0.9553$ that were significant at the 0.05 level. M and T showed a positive correlation of 0.8587 and 0.7314 respectively, however, the results were non-significant. L showed a weak negative correlation of -0.2253, however, the results were insignificant as well.

Far SS and Partnered Swimming: Of the six animals, five showed a non-significant negative correlation between Far SS and Partnered Swimming, where A, M, N, and T showed stronger negative correlation coefficients in the ranges of -0.6685 to -0.8461, and L showed a weak negative correlation of -0.1227. C is the only animal that showed significance at 0.0071 of a strong negative correlation of -0.9671.

Thus, results showed that all six animals' preferred associate for partnered swimming has a strong positive correlation with Parallel SS, compared to non-Parallel SS and Far SS. Now, the question is, during an SS, what is the partnered state of the two dolphins?

Q2: SS as a predictor for Partnered-Swimming

To examine if SS can be a predictor for partnership underwater, a chi-square was conducted. The two categorical variables to be tested here were the synchronous state of surfacing (SS or Solitary

Surfacing) and the partnered state (Partnered or non-Partnered) where both SS and partnered included all of the possible types (Parallel, non-Parallel, and Far for SS; Tight and Loose for Partnered Swimming). Frequencies were summarized in Table 3 along with its calculated chi-square value and p-value. The null hypothesis of this chi-square was that the state of synchrony is not associated with partnered swimming. Results successfully rejected the null hypothesis except for T. Nonetheless, the contingency table showed general patterns where animals tended to SS while in a partnered state than SS in a non-partnered state. On the other hand, when animals performed solitary surfaces, they tended to not be in a partnered state. The anomaly here, T, had a general pattern where partnership did not affect patterns of surfacings; her SS was higher than Solitary Surfacing where the state of partnership did not affect this tendency.

Table 3: Chi-square to examine if the two categorical variables (surfacing behavior and partnered swimming behavior) are independent of each other. Surfacing Behavior can be either SS or Solitary Surfacing, and Partnered Swimming can either be a successful Partnered Swimming -either Tight or Loose- or non-Partnered Swimming.

ID	Surfacing / Partnered-Swimming	SS in Social Space	Solitary Surfacing	Chi-Squared	p-value
A	Partnered Swimming	177	109	62.67	2.44E-15
	non-Partnered Swimming	84	208		
C	Partnered Swimming	223	99	191.53	< 2.2E-16
	non-Partnered Swimming	110	412		
L	Partnered Swimming	122	99	44.69	2.31E-11
	non-Partnered Swimming	78	243		
M	Partnered Swimming	73	103	7.224	7.19E-03
	non-Partnered Swimming	69	174		
N	Partnered Swimming	119	72	98.86	< 2.2E-16
	non-Partnered Swimming	56	252		
T	Partnered Swimming	359	157	1.4067	0.2356
	non-Partnered Swimming	104	58		

Q3: Association between Partnered-Swimming Proximity in triadic AB+C formation and SS

Upon looking at triads, a total of 121 surfacing events happened when animals were in the AB+C formation where two animals are tight partners, and the third animal is the loose partner for the tight pair (see Figure 3). The triads maintained the AB+C formation for a combined duration of 2.75 hours, which accounted for 61% of the overall triadic partnered swimming duration.

Among the surfacing events that occurred while in the AB+C formation, 62 surfacing events were dyadic surfacing events between the Tight pair (animals A and B), 11 were dyadic surfacing events between the Loose pair (animal A&C and B&C), and 47 surfacing events involved all three members of the triad surfacing together in synchrony (as shown in Figure 6).

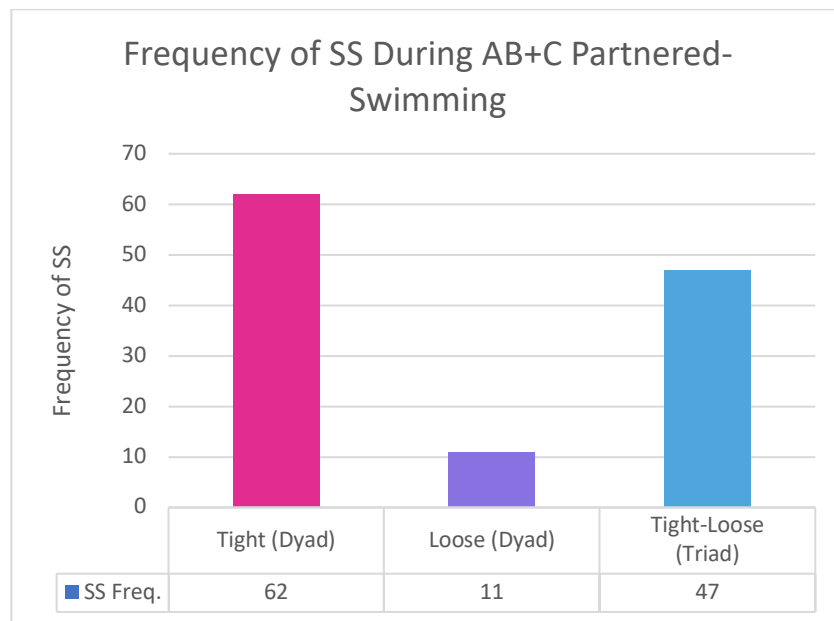


Figure 5: Bar plot of Frequency of SS during an AB+C Partnered-Swimming formation.

DISCUSSION

Overview of the Findings

Results from this study indicate three findings. 1) Upon investigating the relationship between preferred associate per subject for the three types of SS and partnered swimming, a positive correlation was evident between Parallel SS and Partnered Swimming for all six animals. 2) Our findings indicate that close proximity Parallel synchronous surfacing does, in fact, serve as a predictor of partnered swimming both before and after the surfacing event. 3) Lastly, results conclude that proximity within the partnered state affected the AB+C triadic partnered state, where the Tight dyad tended to SS the most, followed by the Tight-Loose triad, followed by the Loose dyad that SS-ed the least.

Relationship within subjects: the existence of cohorts, kinship, and dominance

Results of the adult-juvenile cohort and sub-adult cohort further support the existence of partnership or cohort where animals have bonded partners (Owen & Caffee, 2002) and appear to facilitate affiliative behavior reinforcing social bonds (Connor et al., 2006a; Sakai et al., 2010). This was evident both in surfacing data as well as partnered data, where there were higher rates of Parallel synchronous surfacing between pairs in the same cohort and a higher percentage of partnered duration within members of the same cohort.

The mother-daughter relationship between A and T exhibited the highest rates of partnered swimming, with both individuals displaying a mutual preference for each other, in line with the well-documented bond between mothers and calves involving synchrony and association (Mann & Smut 1999; Fellner et al., 2006; Wells 1991).

Additionally, the social dynamic within the subjects may be a factor that has caused a failure in rejecting the null hypothesis for the chi-square analysis for T. Amongst the subjects, T has the longest

residency of 14 years and is the mother of two other animals where trainers claimed her to be the dominant animal, all of which are status conveying points. Thereby, it may be that she is more involved in synchrony due to her being in a higher social status than others in the habitat, causing the animal to be an attractive associate for synchrony.

Implications on Proximity

Upon looking at the big picture from the general findings, we can see the significance of proximity and orientation on synchrony and partnered swimming where the positive correlation suggested a high possibility that pairs that perform higher rates of Parallel SS (which is a parallelly orientated close-proximal synchrony) is more likely to also perform higher percentages of partnered swimming. The significance in proximity is consistent in triadic analysis of AB+C formation where results indicated higher rates of synchronous surfacing between pairs in closer proximity. These findings align with previous studies on synchrony, proximity, and orientation (Sakai et al. 2009) and suggest that synchrony proximity can indicate the level of synchrony, where animals that are closer swimming closer in proximity can display higher levels of synchrony, also evidenced by the shorter latency observed in parallel synchronous surfacing in this study.

Chained Events

Chain events were fully omitted from this project, but we must recognize that there were 915 chained surfaces collected in this project which encapsulates 13% of the total. A possible explanation as to why chains occur may be that chained scenes contain a mix of synchrony and imitation where surfaces that happen after the initial synchrony window may have been performing “mimicry” (Tomasello, 1999). In other words, it is suggested that animals after the initial 2.5 synchrony window may be reacting to their “demonstrator”. Furthermore, an elongated chain could thus be suggested that

animals may have synchronized their surfacing alternatively as a result of modifying their behavior to respond to the activity of members who were performing imitation. This type of motor synchronization is defined as “kinesthetic imitation” (Kuczaj & Yeater, 2006) where in the case of chains, mimicking animals match the demonstrator’s behavior. The distinction between whether the animal’s surfacing was a reaction to mimicry versus a synchronized act, cannot be made in this project. However, the phenomenon of chained events is strongly suggested to be considered a distinct behavior due to its frequency of occurrence. Thereby, further investigation on its possibility of happening by chance through permutation is strongly recommended to first, understand the likelihood of such events to happen.

Implications of the Low Surfacing Rate

While the average surfacing rate is reported to range from 2.6-2.9 surfaces /min, or 156-172 surfaces/hour (Barbara 1999; Miketa 2018), results from this study show an average of 86 surfaces/hour. Despite this difference, the standard deviation is at 6.2 surfaces/hour, showing uniformity among the subjects of this study. One major factor that could be driving the surfacing rates down may be the differences in surfacing definitions based on the methods used in this study. Although lingering animals present in social space were scored, and later omitted, lingering animals were never scored in the first place possibly causing the lower surfacing rate. Another possibility is that animals here are under human care where observations were taken between shows, in comparison to the average surfacing rates that are reported on wild animals where there may be more metabolic demands for higher breathing rates. Despite this difference, the uniformity contributes to a factor ruling out subject-by-subject tendencies, promising a more unbiased evaluation when moving forward.

Limitations, Improvements, and Applications

The topic of limitations due to the subjects being under human care is inevitable. While results cannot make direct suggestions of population behavior in wildlife, this study became approachable because of the beneficiaries of studying animals under human care and most importantly, some of the findings made in this study aligned with those that were studied on wild populations, allowing us to make implications not on the behavior of these animals, but more importantly, the capabilities of Bottlenoses dolphins and the nature in synchronous acts.

One aspect that needs to be mentioned is the difference in the coverage of Social Space, Tight-Partnered Swimming, and Loose-Partnered Swimming, shown in Figure 3. Due to the nature of the datasets, in that this study is a combination of three independently collected sets of data, there is more longitudinal coverage of Social Space than the range of Partnered Swimming. Thereby, surfaces that were counted to be within Social Space contained ones that were out of bounds for Partnership purely due to the defining range differences. Consequently, there will be an over-representation of Parallel or Non-Parallel SS that was not partnered. Thus, the non-agreement in the range definition is biased to show more SS that were non-partnered. Yet, despite the skew causing a disadvantage. results indicated otherwise and were able to successfully reject the null hypothesis on the chi-square analysis. Thus, another speculation as to why T failed to reject the null hypothesis of partnered state and synchronous state having no correlation can perhaps be tied to this faulty definition disagreement. Therefore, in future investigations, it is highly suggested to use the same parameter in setting the ranges.

For the future of synchrony investigation, I must emphasize the possibility of the indicative role of synchrony that were not in close proximity, that is, the Far SS, especially since Far SS has continued to not show much significance in this study. Perhaps Far SS may be a signal that is a precursor of

partnership, or perhaps it's a signal to temporarily break a partnership. A more detailed sequential analysis of the timing of synchrony and partnership is strongly suggested to unravel the understudied sector of non-proximal synchrony, as further studies will enrich in measuring affiliative prosocial behaviors of Bottlenose dolphins.

Acknowledgements

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APPENDIX A

Table 4: This table shows 15 dyads amongst the 6 different dolphins, A, C, L, M, N, and T for their duration for Co-Presence, % Loose Partnered-Swimming, and % Tight Partnered-Swimming. The Green indicates that the members of the dyad are inter-cohort members whereas Red indicates dyad in mixed-cohorts.

Dyad		Co-Pres. Duration	% Loose Duration	% Tight Duration
C	T	47100	28.61%	8.34%
M	N	35732	24.49%	22.74%
A	T	48177	17.23%	20.36%
A	C	44225	15.69%	0.86%
L	T	45192	13.50%	22.54%
C	L	42332	13.15%	1.05%
A	L	41682	3.99%	0.79%
A	M	22628	2.87%	1.10%
A	N	23001	2.48%	0.17%
M	T	22172	1.92%	0.79%
N	T	22491	1.18%	0.11%
L	M	20317	1.11%	0.15%
L	N	20767	0.99%	0.10%
C	M	23875	0.50%	0.10%
C	N	24033	0.35%	0.06%

APPENDIX B

Table 5: The % Partnered Swimming, Parallel SS Rate (frequency/hour), non-Parallel SS Rate (frequency/hour), and Far SS Rate (frequency/hour) on the left side were used to run a Pearson's Correlation Test for each subjects on the right side of the table. The Correlation Estimate along with its p-value are summarized below.

Dyad		% Partner Swim. (hrs)	Para Rate (freq / hr)	non-Para Rate (freq / hr)	Far Rate (freq / hr)	Pearson's Correlation Test						
A	C	16.55	5.86	1.55	10.58	Focal = A		Para	non-	Far		
	L	4.79	1.55	1.04	8.46	Correlation	Partner Swim.	0.9595	0.9596	-0.7050		
	M	3.98	2.07	1.11	10.18	Estimate						
	N	2.65	2.82	0.63	10.64	p-value						
	T	37.59	16.74	2.02	6.58						0.0097	0.0097
C	A	16.55	5.86	1.55	10.58	Focal = C		Para	non-	Far		
	L	14.20	3.91	0.85	10.63	Correlation	Partner Swim.	0.9449	0.9723	-0.9671		
	M	0.61	0.45	0.00	14.78	Estimate						
	N	0.42	0.60	0.00	13.33	p-value						
	T	36.91	14.14	1.99	8.79						0.0154	0.0055
L	A	4.79	1.55	1.04	8.46	Focal = L		Para	non-	Far		
	C	14.20	3.91	0.85	10.63	Correlation	Partner Swim.	0.9305	-0.2253	-0.1227		
	M	1.26	0.71	0.71	8.68	Estimate						
	N	1.08	1.39	0.69	9.71	p-value						
	T	36.01	18.24	0.64	8.36						0.0218	0.7155
M	A	3.98	2.07	1.11	10.18	Focal = M		Para	non-	Far		
	C	0.61	0.45	0.00	14.78	Correlation	Partner Swim.	0.9916	0.8587	-0.6685		
	L	1.26	0.71	0.71	8.68	Estimate						
	N	47.23	24.78	1.71	7.05	p-value						
	T	2.71	0.49	0.49	10.07						0.0009	0.0624
N	A	2.65	2.82	0.63	10.64	Focal = N		Para	non-	Far		
	C	0.42	0.60	0.00	13.33	Correlation	Partner Swim.	0.9969	0.9342	-0.8302		
	L	1.08	1.39	0.69	9.71	Estimate						
	M	47.23	24.78	1.71	7.05	p-value						
	T	1.29	0.16	0.48	10.40						0.0002	0.0201
T	A	37.59	16.74	2.02	6.58	Focal = T		Para	non-	Far		
	C	36.91	14.14	1.99	8.79	Correlation	Partner Swim.	0.9834	0.7341	-0.8461		
	L	36.01	18.24	0.64	8.36	Estimate						
	M	2.71	0.49	0.49	10.07	p-value						
	N	1.29	0.16	0.48	10.40						0.0026	0.1579

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