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ORIGINAL PAPER

Synchrony during aggression in adult male Atlantic spotted dolphins *(Stenella frontalis)*

Alyson J. Myers [1,2] · **Denise L. Herzing** [1,2] · **David F. Bjorklund** [1]

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Abstract Synchrony among Atlantic spotted dolphins (*Stenella frontalis*) is crucial for successfully overcoming bottlenose dolphins (*Tursiops truncatus*) during interspecies aggression (Cusick and Herzing 2014). The present study examined synchrony in adult Atlantic spotted dolphins during aggressive encounters with bottlenose dolphins. Across group size, aggressive behaviors increased preceding synchrony, peaked during synchrony, and decreased dramatically after synchrony. Although smaller groups (< 10 dolphins) became synchronous more frequently than larger groups (> 10 dolphins), larger groups remained synchronous longer; however, smaller groups exhibited greater aggressive behaviors during synchrony, suggesting that additional aggressive behaviors may be necessary to compensate for the smaller group size, whereas larger groups may be able to rely on synchrony with less aggression. Disorganized squawk bouts synchronized as physical synchrony began, but only if coupled with escalating aggression.

Keywords *Stenella frontalis* · Synchrony · Aggression · Atlantic spotted dolphin

Introduction

Cooperation and working together to reach a common goal are important and valuable traits of a social species. Part of this cooperation includes the coordination and synchronization of specific behaviors. Synchronization of behaviors occurs when two or more individuals are performing the same behaviors at the same time (Connor et al. 2006), whereas coordination includes using different behaviors to obtain a shared goal (Boesch 2002). Coordination has been observed in terrestrial animals as a method of cooperative defense, coordinated attacks, and during play (Boesch 2002; Mech and Boitani 2003; Mech 2007). For example, chimpanzees *(Pan troglodytes)* engage in coordinated behaviors as a method of cooperative defense and coordinated attacks (Boesch 2002). Wolves *(Canis lupis)* have also been observed to lead coordinated attacks that allow them to be more successful (Mech and Boitani 2003; Mech 2007). The use of this coordination of behaviors can improve the attackers' success with capturing prey or defeating competition. Synchrony can serve a similar function as cooperation in other species, such as the synchronization of aggressive behaviors in Atlantic Spotted dolphins (*Stenella frontalis*) during interspecies aggression to overcome bottlenose dolphins (*Tursiops truncatus*) (Cusick and Herzing 2014) or the synchronization of pulling behaviors in captive bottlenose dolphins to reach the common goal of obtaining a food reward in a container (Kuczaj et al. 2015). Some other noticeable examples of synchrony that serve different goals, such as predator avoidance and mate attraction, are the movements of schools of fish (Pitcher and Parrish 1993), synchronous flashing of fireflies (Buck 1938), male fiddler crabs (*Uca annulipes*) waving their claws in synchrony to attract mates (Backwell et al. 1999), and Western Grebe *(Aechmophorus occidentalis)* courtship displays (Nuechterlein and Storer 1982).

Fireflies (*Coleoptera: Lampyridae)* use synchronous bioluminescent flashes as a signal. Male North American fireflies (*Photinus carolinus*) flash in synchrony with millisecond precision (Copeland & Moiseff 1995). The synchrony of the

✉ Alyson J. Myers
amyers15@fau.edu

[1] Department of Psychology, Florida Atlantic University, Bldg. 12, 777 Glades Road, Boca Raton, FL 33431, USA

[2] Wild Dolphin Project, P.O. Box 8436, Jupiter, FL 33468, USA

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flashing helps a female recognize a conspecific male by removing potential visual clutter that could occur from other flashing males (Moiseff & Copeland 2010). When females were placed in a virtual environment that contained artificial males that flashed at a variety of degrees of synchrony, the females responded significantly more to the synchronous flashes than the asynchronous flashes (Moiseff & Copeland 2010).

Synchrony is also important in reproduction for another species, the Western Grebe. Western Grebe pairs partake in a display called a Weed-dance. This Weed-dance involves close synchrony between the pair. The two birds approach each other with weeds in their beaks until they are less than a body-length apart and then rise up breast to breast in synchrony (Nuechterlein and Storer 1982). The dance is over when one bird discards its weeds and shakes its head quickly. The Weed-dance most likely evolved from nest building. The mutual manipulation of the weeds that are often used in nest building may indicate the willingness to pair (Nuechterlein and Storer 1982).

In marine mammals, synchronous behaviors have been observed in a range of contexts. Captive bottlenose dolphins were observed to demonstrate synchronous swimming in response to a novel stimulus placed in their tank (McBride and Hebb 1948). Killer whales *(Orcinus orca)* were also observed to surface synchronously during coordinated feeding on herring (Similä 1997). Synchronous surfacing in Indian Ocean bottlenose dolphins *(Tursiops aduncus)* is also related to alliance membership, as reflected by the fact that known male alliances were more likely to surface in synchrony (Connor et al. 2006). Synchronous swimming has also been observed as an anti-predator function in Spinner dolphins *(Stenella longirostris)* (Norris and Schilt 1988). Bottlenose dolphins have also been observed to partake in synchronous behaviors during foraging (Bel'kovich et al. 1991). Both bottlenose and Atlantic spotted dolphins have been observed to form a synchronous school as a fear response to predators and novel situations (Fellner et al. 2012). Synchrony is also evident among male bottlenose dolphins during herding or mating encounters (Cusick and Herzing 2014).

Synchronous swimming provides a hydrodynamic advantage versus swimming alone. It can also help to create a sensory integration system that can facilitate the detection and avoidance of predators (Fellner et al. 2012). This means that by moving synchronously, the dolphins are acting as a single, hyper-sensitive organism (Norris and Dohl 1980). This would allow rapid transmission of information through subtle movements, sounds, and eye gaze that would otherwise not be easily transmitted if not in a tight synchronous formation (Norris and Dohl 1980). This could benefit dolphins by aiding in communication and coordination during an aggressive encounter.

Synchronous behaviors may also be important in social affiliations and cultural transmission of information (Fellner et al. 2012). Moving in synchrony can strengthen male coalition bonds (Fellner 2000). It can advertise to other males the membership of their coalition and demonstrate hierarchical relationships. Dominant males may regularly enforce synchrony while subordinate males may initiate synchrony to demonstrate their submission or to gain favor with dominant males (Fellner 2000).

Synchrony in aggressive encounters in Atlantic spotted dolphins

There are differences in spotted dolphin behaviors during interspecies aggression and intraspecies aggression. During interspecies aggression, spotted dolphins used more biting, chasing, and contact behaviors and used more display behaviors during intraspecies aggression (Volker 2016). This indicates that they are adjusting their aggression tactics based on the type of aggressive encounter. The presence of synchrony during interspecies aggression in wild Atlantic spotted dolphins determined whether or not dynamic shifts were in favor of the spotted dolphins (Cusick and Herzing 2014). A dynamic shift is defined as a change in which species are the aggressor and victim. A dynamic shift was determined to be in favor of one species over the other when one species that was originally the victim became the aggressor or vice versa. Cusick and Herzing (2014) focused on factors, such as the presence of synchrony, that influence the outcome of aggressive encounters. The mechanics and processes of how synchrony begins, is achieved, or thwarted were not examined, only the presence or absence was noted.

The advantages stated above of synchrony in an array of situations has been demonstrated in a number of species including wild Atlantic spotted dolphins, however the specific mechanics of synchrony in this species have not been studied. As it has been established that synchrony is such an important aspect of interspecies aggression, it is extremely valuable to characterize the exact behaviors that occur within a synchronous group. Previous studies that observed and analyzed synchrony in dolphins were mostly captive (McBride and Hebb 1948) or analyzed only the surface behaviors (Connor et al. 2006; Similä 1997). While extremely valuable, underwater observations with free-ranging animals were missing from these earlier studies. The current study fills this void and provides insight into the underwater behaviors and vocalizations of a group of wild dolphins during aggressive synchrony. In addition, by establishing a baseline for adult synchrony, future research will be able to observe the process by which juvenile dolphins develop and learn this valuable skill.

Current study

The objective of the present study was to describe and examine the mechanics of synchrony in adult male Atlantic spotted dolphins during aggressive encounters with bottlenose dolphins. As synchrony was established to be a key factor in the success of Atlantic spotted dolphins during interspecies aggression (Cusick and Herzing 2014), it is important to examine the physical behaviors and vocalizations in synchrony to understand the advantages and power of this valuable skill. To this end, we examined the behaviors before synchrony, during synchrony, and after synchrony. Three aggressive behavioral classes (display behaviors, contact behaviors, and pursuit behaviors) and events within these classes were analyzed. Bouts of vocalizations (squawks and synchronized squawks) were also analyzed. The duration of synchrony was also examined.

We predicted that there would be differences in the frequency of aggressive behaviors during synchronous aggression and nonsynchronous aggression, as synchronous aggression is an escalated state during interspecies aggression. As spotted dolphins have been seen to change their aggression tactics based on group composition (Volker 2016), we also predicted there would be further differences in the frequency of aggressive behaviors and duration of the synchronous event as a function of group size. Using the behavioral classes and events, we were able to examine the differences in the amount of aggressive behaviors exhibited before synchrony begins, during synchrony, and immediately after synchrony. It is reasonable to predict that there would be more behavioral events before and during synchrony than after synchrony as the aggressive encounter is likely resolved. Using lag sequential analyses, probabilities of behavioral classes and vocalizations occurring with the onset and end of synchrony were used to describe the relationship between physical behaviors and vocalizations with synchrony.

Methods

Study population

This study was conducted with the Wild Dolphin Project, which has been studying two sympatric species of dolphins, the Atlantic spotted dolphin *(Stenella frontalis)* and the Atlantic bottlenose dolphin *(Tursiops truncatus),* in the Bahamas on the north area of Grand Bahama Island since 1985. This unique environment allows for clear observation of the animals in and out of the water. Underwater observation is done by in-water experimenters using snorkeling equipment. Over 200 individual Atlantic spotted dolphins have been identified along with their sex, age class, maternity, paternity, and population genetics (Herzing 1996, 1997). There are four age classes used to describe Atlantic spotted dolphins; two-tone, speckled, mottled, and fused. Two-tone dolphins are neonates or calves aged 1–3 years. Speckled dolphins are juveniles aged 4–8 years. Mottled dolphins are young adults aged 9–15 years. Finally, fused dolphins are adults above the age of 15 years (Herzing 1997). Over 200 bottlenose dolphins have also been identified, aged, and sexed when possible. Sex for both species is determined by observation of the genital slit. The study population for this research consisted of adult male Atlantic spotted dolphins. Adults were considered to be of mottled and fused age classes.

Study site

The study site for the Wild Dolphin Project is located on the western edge of Little Bahama Bank off Grand Bahama Island (ranging from 26°42′ N, 79°00′W to 27°15 N, 79°08′ W) and most recently off Bimini in the Bahamas. These locations are composed of shallow waters (ranging 6–16 m) that are surrounded by deeper waters (>500 m). The study site is composed of a white sandy bottom scattered with patches of reef, rock, and seagrass (*Thalassia testudimum).* The shallow waters provide clear visibility, which provides optimal viewing of the dolphins and their behaviors.

Data collection

All video used in the present study was archival. The Wild Dolphin Project has collected video data on wild Atlantic spotted dolphins and bottlenose dolphins during every summer (May – September) since 1985 aboard the R/V Stenella (a 20-m live-aboard catamaran) from 0700 to 1900 daily. Every encounter has been documented using photographs, video, and written data. Written data includes GPS location, group size, group composition, behavioral context, time, habitat, and environmental data. An encounter starts when underwater observation of the dolphins begins and ends when the underwater observation ends. Underwater video and photographs are taken to identify the individuals and document the behavior. Vocalizations are also recorded using a hydrophone that is attached to the video equipment (e.g. Sony XR 550, GoPro Hero 4). Ad lib, focal sampling, and behavioral event scanning methods were used to collect the video data (Herzing 1996; Herzing et al. 2003).

Behavioral definitions

Behavioral analysis

This study focused on examining aggressive events that included bouts of synchrony. Not all aggressive encounters include synchrony, but the purpose of this study was to examine aggressive episodes that included synchronous bouts. Synchrony was defined as more than one animal performing the same behavior in the same direction towards the same individual at the same time. As synchrony in this study was in the context of aggression towards another species, there is a directional component. Nonsynchrony was defined as animals doing different behaviors in different directions. Behaviors and vocalizations during synchrony were recorded for frequency of occurrence to examine whether there are differences when the dolphins are synchronous versus when they are not synchronous. The physical behaviors and vocalizations before and after the beginning and ending of synchrony were also examined to determine a process of synchrony during aggressive encounters with bottlenose dolphins. This allowed the study of behaviors that typically lead into a synchronous event, behaviors during a synchronous event, and behaviors that occur after disengaging in synchrony. In order to consider a behavior as occurring before or after synchrony, it must have occurred within 5 s of synchrony beginning or ending. During aggressive encounters, Atlantic spotted dolphins engage most commonly in open mouth displays, chasing, and biting (Cusick and Herzing 2014). As synchrony typically occurs during aggressive interactions, these are the behaviors that we focused on. Acoustics were also examined to assess the role particular vocalizations have during behaviorally synchronous events.

Video analysis

Video sequences from 1991 to 2004 from the Wild Dolphin Project video archives were used in this analysis. For the content of a video to be considered for inclusion in this data set, the video had to include (1) spotted dolphin adult male aggression against one or more bottlenose dolphins and (2) show at least one behaviorally synchronous event. The synchronous event had to be shown from its beginning to its end and was measured as a bout using a start time and end time. Synchrony was considered to end when the dolphins dispersed from their synchronous group. Seven videos, totaling 164.68 min, matched these criteria and were analyzed. Within these seven videos, there were 60 synchronous events. This study used the software Observer XT Version 7.0 for Windows to code all aggressive behaviors in the videos. An ethogram (see Table 1) was developed to code for the behaviors that were analyzed. Refer to the ethogram for operational definitions of specific behaviors and vocalizations.

Three aggressive behavioral classes were analyzed; display behaviors, contact behaviors, and pursuit behaviors. Within these behavioral classes there were specific behavioral events. Display behaviors included open mouth displays, jaw claps, and bubble rings (torus). Contact behaviors included tail slaps, biting, head to head behavior, and pinning a dolphin to the seafloor. Pursuit behaviors included chasing and charging. In addition to the scored behavioral events, the beginning and end of synchrony was scored. The presence of dolphin vocalizations, as described in Herzing (2015), were scored as bouts with a start and stop time in order to extract the durations. Squawk bouts, synchronized squawk bouts, and conflict vocalizations were scored.

We further examined physical behaviors and duration of a synchronous state as a function of the size of the group of dolphins. The group size was recorded for every synchronous event. The group sizes recorded were from 2 to 5 dolphins, 6–10 dolphins, 11–15 dolphins, 16–20 dolphins, and 20+ dolphins. A range was used because dolphin groups are fluid, and individuals often joined and left the synchronous group during a bout. Initial analyses were first at the level of the 5 sub-categories, but for simplified analyses, specific group sizes were collapsed into 10 or fewer dolphins and 11 or more dolphins.

To compute intra-rater reliability, 28% of the videos were randomly selected to be scored again by the primary observer. To compute inter-rater reliability, 20% of the videos were randomly selected to be scored by a secondary observer who also studies aggression. All aggressive behaviors were scored and compared to compute reliability. To calculate inter-rater and intra-rater reliability, a Pearson's r correlation was calculated. A correlation of .70 and above was considered strong inter-rater and intra-rater reliability. Intra-rater reliability was above .70 and considered strong reliability at .87. Inter-rater reliability was also considered strong at .88.

Statistical analyses

Statistical analyses, discussed below, examined (1) the frequency of occurrence of each behavioral class during synchrony and nonsynchrony; (2) the frequency of each behavioral class during synchrony, based on group size; (3) differences in duration and frequency of synchrony associated with group size; (4) the probability of each behavioral class and vocalizations occurring with synchrony; and (5) vocalizations and their relationship with synchrony and aggressive behaviors. The statistical software SPSS Version 22 and Observer XT Version 7.0 formatted for Windows were used to conduct these analyses.

The total time dolphins spent nonsynchronous in aggressive encounters that contained bouts of synchrony was longer (147.27 min) than the total time spent synchronous in these aggressive encounters (17.41 min). Using the frequency of occurrence of each behavioral event in each aggressive encounter and the duration of time, a rate per minute was calculated for each behavioral event during nonsynchronous aggression and synchronous aggression. This was done in order to analyze the frequency of behavioral events in proportion to the time spent synchronous and nonsynchronous in each aggressive encounter. Independent samples t-tests were then used to examine if there were differences in the rate per minute for each behavioral class (display, contact, and pursuit) during nonsynchronous aggression and synchronous aggression.

An independent samples t-test was used to examine if there were differences in the duration of a synchronous state as a

Table 1 Behavioral ethogram showing the behavioral classes and behavioral events within the classes

Behavioral Classes	Behavioral Events	Description
Display		
	Open Mouth	Dolphin or group opens mouth towards another dolphin or group
	Jaw Clap	Dolphin opens and shuts jaw rapidly towards another dolphin
	Torus	Dolphin blows a bubble ring
Contact		
	Tail Contact	One dolphin or group swipes or makes contact with another dolphin or group using tail
	Bite	One dolphin bites or rakes another dolphin on body or tail
	Head to Head	Dolphin or group takes head to head position with another individual or group
	Pin	Dolphin or group of dolphins pins another to the bottom
Pursuit		
	Chase	One or a group of dolphins chases another individual or group
	Charge	Two or more dolphins charge towards each other in head to head format, occasionally making contact
Synchronous Behaviors		
	Begin Physical Synchrony	All individuals begin to perform the same behavior towards the same individual at the same time
	End Physical Synchrony	Individuals perform different behaviors in different directions towards different individuals
Vocalizations		
	Squawk	Broad-band vocalization with distinct tonal sound
	Synchronized Squawk	More than one dolphin squawks at the same time

function of group size (10 or fewer vs. 11 or more). Differences in the duration of synchronous behavior as a function of group size was also demonstrated via correlational analyses.

Differences in the number of behavioral events immediately preceding, during, and after synchrony across group size were also analyzed using paired samples *t*-tests. In order to consider a behavior as occurring immediately before or after synchrony, it must have occurred within 5 s of synchrony beginning or ending. This ensures that the behaviors are indeed associated with the particular aggressive event that contained synchrony. The data were also normalized to the number of dolphins present by calculating a rate of behavior per dolphin using average group size.

The probabilities of behavioral classes and vocalizations occurring immediately before synchrony begins, immediately after synchrony begins, immediately before synchrony ends, and immediately after synchrony ends were analyzed using lag sequential analyses. This analysis was done to examine the physical behaviors and vocalizations that occurred at a high probability with the onset and ending of synchrony.

An independent samples *t*-test was used to test whether there was a difference in the durations of squawk bouts that became synchronized squawk bouts compared to squawk bouts that did not become synchronized. Finally, a binomial sign test was conducted to examine if there were significant differences in behavioral events and behavioral classes that occurred during squawk bouts that became synchronized that led to physical synchrony and those that did not lead to physical synchrony.

Results

A total of 60 synchronous events were analyzed across the seven videos. Aggression was observed in approximately 84% of all video analyzed, and synchronized behavior was observed in approximately 10% of all aggressive time. The dolphins were not aggressive during 16% of the analyzed video time. The most frequently observed behavioral classes across all events were pursuit ($N = 99$), contact ($N = 66$), and display ($N = 60$). The most frequent vocalization across all events was squawk bouts ($N = 104$).

Behaviors during synchrony

Rates of contact, pursuit, and display behaviors for synchronous and nonsynchronous aggression are presented in Table 2. A rate per minute for each behavioral class occurring during aggression in each video was calculated. Rate per minute of contact behaviors (tail contact, bite, head to head, pin) was significantly higher during synchronous aggression than during nonsynchronous aggression, $t(6) = 2.81$ $p < .05$. Rate per minute of pursuit behaviors (chase, charge) was also significantly higher during synchronous aggression than during nonsynchronous aggression, $t(6) = 3.71$, $p < .05$. Differences in rate per minute of display behaviors (open mouth, jaw clap, torus) between synchronous and nonsynchronous aggression were not significant, $t(6) = 1.77$, $p = .126$. This nonsignificant effect was likely due to the relatively small number of observations ($N = 60$) and high variability of display behaviors. When the behavioral classes were combined, the rate per minute of the aggressive behaviors were significantly higher during synchronous than nonsynchronous aggression, $t(6) = 4.58$, $p < .05$.

Frequency and duration of synchrony based on group size

There were a total of 60 synchronous events analyzed across videos, 39 involving groups of 10 or fewer and 21 involving groups of 11 or more. Given the presence of synchrony, groups of 11 or more dolphins remained synchronous ($M = 24.63$ s, SD = 18.60) for longer than groups of 10 or fewer dolphins ($M = 13.29$ s, SD = 10.32), $t(58) = -3.04$, $p < .05$. However, given there was synchrony, groups of fewer than 10 dolphins became synchronous more frequently ($N = 39$) than groups of more than 11 dolphins ($N = 21$), binomial test, $p = .027$.

A Pearson's r correlation between group size (2–5 animals per group; 6–10 animals per group; 11–15 animals per group, 16 and more animals per group) and duration of synchronous events was significant, $r = .437$, $p < .0001$. As group size increased, the duration of the synchronous event also increased.

Frequency of behaviors before, during, and after synchrony

Mean pursuit, contact, and display behavior before, during and after synchrony are shown in Table 3. There were no significant differences in the aggressive behaviors between behavioral classes before, during, and after synchrony (pursuit = .055; contact = .054; display = .081) There were, however, significant differences within each behavioral class before, during, and after synchrony. For pursuit behaviors, levels were significantly greater during synchrony than both before or after synchrony, $ts(59) \geq 2.05$, $p < .05$, with the latter two not differing from one another, $t(59) = 1.28$, $p = .21$. There were also significantly more contact behaviors during synchrony than both before and after synchrony, $ts(59) \geq 2.82$, $p < .05$ with the latter two not differing from one another, $t(59) = 0.19$, $p = .85$. For display behaviors, rates were greater during synchrony than after, $t(59) = 2.58$, $p < .05$. All other contrasts were nonsignificant.

When pursuit, contact, and display behavioral classes were combined, there were significantly more aggressive behavioral events during synchrony per dolphin than immediately before and after synchrony, $t(59) = 2.99$, $p < .05$. While there was a higher number of behaviors before synchrony than after synchrony, the difference was not significant $t(59) = 1.94$, $p = .057$. This demonstrates a pattern of behaviors with the amount of aggressive behavioral events being high before synchrony, highest during synchrony, and lowest after synchrony.

Frequency of behaviors based on group size

Group size had a significant effect on the amount of all behavioral events combined occurring with synchrony (see Fig. 1). The results trended towards there being more behavioral

Table 2 Means and standard deviations for the rate per minute of behavioral classes (contact, pursuit, and display behaviors) during nonsynchronous aggression and synchronous aggression. The N of each behavioral class is also shown. Significance ($p < .05$) is indicated by an asterisk

Behavioral Classes	Nonsynchronous Aggressive Events N	Nonsynchronous Aggression	Synchronous Aggressive Events N	Synchronous Aggression
Contact Behaviors	49	M = .41* SD = .28	17	M = 1.05* SD = .46
Pursuit Behaviors	78	M = .57* SD = .25	21	M = 1.59* SD = .75
Display Behaviors	35	M = .30 SD = .20	25	M = 1.50 SD = 1.85
Total Behavioral Classes	162	M = .43* SD = .21	63	M = 1.38* SD = .66

Table 3 Means and standard deviations for pursuit, contact, and display behaviors occurring before, during, and after synchrony

Behavioral Class	Before Synchrony	During Synchrony	After Synchrony
Pursuit Behaviors	M = .01	M = .04	M = .005
	SD = .04	SD = .10	SD = .03
Contact Behaviors	M = .008	M = .04	M = .006
	SD = .03	SD = .08	SD = .03
Display Behaviors	M = .02	M = .06	M = .001
	SD = .09	SD = .17	SD = .009
Total Behaviors	M = .04	M = .14	M = .01
	SD = .10	SD = .25	SD = .07

events preceding synchrony for smaller (10 or fewer dolphins) groups (M = .08, SD = .16) than the larger groups (M = .01, SD = .02), $t(20) = 2.05$, $p = .054$. There were significantly more behavioral events per dolphin during synchrony in smaller groups (M = .25, SD = .35) versus larger groups (M = .07, SD = .09), $t(20) = 2.19$, $p < .05$. Although the absolute frequency was low, there were significantly more behaviors occurring after synchrony in the larger groups (M = .01, SD = .03) than in the smaller groups (M = .00, SD = .00), $t(20) = -2.14$, $p < .05$. As seen in Fig. 1, both small and large groups of dolphins followed a similar pattern of behaviors, escalating before synchrony, peaking during synchrony, and decreasing dramatically after synchrony. However, smaller groups of dolphins exhibited a greater number of aggressive behaviors than the larger groups.

Probability of behaviors and vocalizations occurring with synchrony

Table 4 presents the probabilities of pursuit, contact, display behaviors, and vocalizations occurring before and after synchrony. Lag sequential results indicated that there was a high probability of a pursuit behavior, a high probability of a display behavior, and a high probability of a contact behavior occurring immediately before synchrony. The probability of a pursuit behavior occurring immediately after synchrony had begun was also high. Display behavior had a high probability of occurring immediately after synchrony had begun and contact behavior diminished. Furthermore, the probability of a pursuit behavior just before the end of synchrony was high and after the end of synchrony was also high. Display

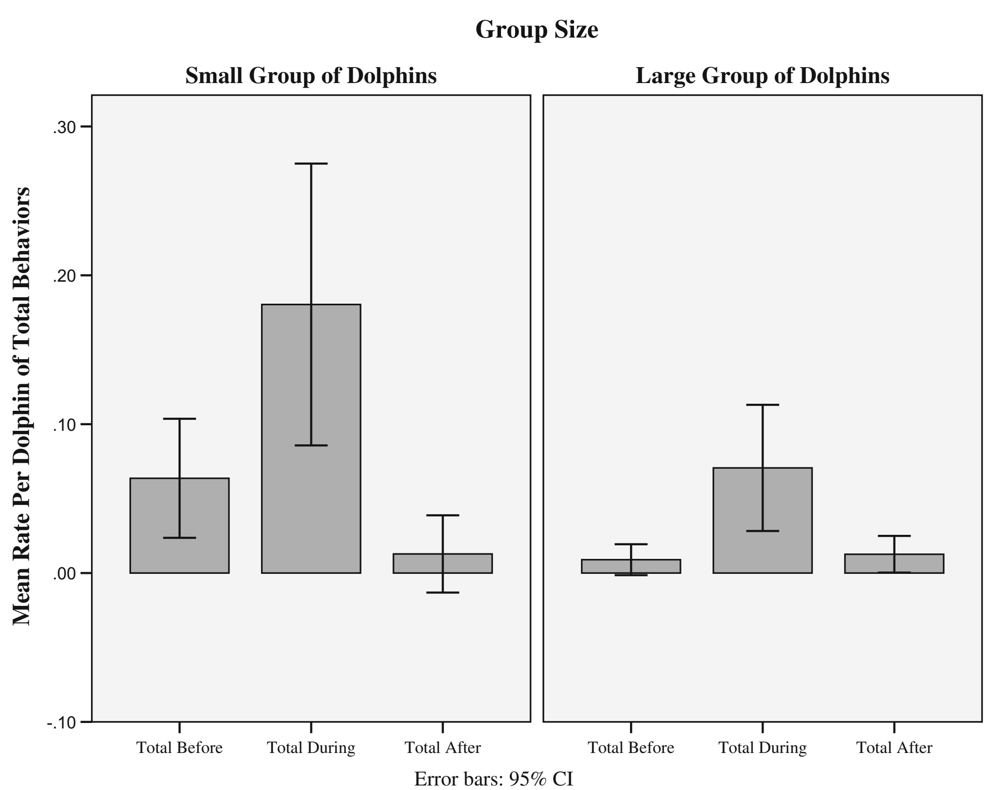

Fig. 1 The rate per dolphin of observed behavioral classes before, during, and after synchrony separated by group size, error bars are at 95%

Table 4 Probabilities of pursuit, contact, and display behaviors and vocalizations occurring before and after synchrony

	1 Before Begin Synchrony	1 After Begin Synchrony	1 Before End Synchrony	1 After End Synchrony
Pursuit				
Total Pursuit	.10	.21	.08	.16
Display				
Total Display	.34	.15	0	.02
Contact				
Total Contact	.12	.02	.08	.04
Vocalizations				
Squawk Bout Begins	.08	.06	.10	.16
Squawk Bout Ends	.02	.04	.02	.19
Synchronized Squawk Bout Begins	.41	.21	.05	0
Synchronized Squawk Bout Ends	.03	.08	.40	.14

behaviors occurring before the end of synchrony had a very low probability of occurrence and a low probability of occurring after synchrony had just ended. The probability of occurrence of contact behaviors were similarly low before the end of synchrony and after synchrony had ended. The probability of occurrence is in agreement with the observed frequencies in that aggressive behaviors tended to occur before synchrony had begun, escalate during synchrony, and diminish with the end of synchrony.

The probability of a synchronized squawk occurring one state lag before synchrony was .41 and the probability of occurring one state lag after synchrony was .21, making the combined probability of a synchronized squawk occurring with the beginning of synchrony very high at .62. In addition, the probability of a synchronized squawk ending one state lag before synchrony ended was .40 and one state lag after synchrony ends was .14, making the combined probability of synchronized squawks ending with the end of synchrony also very high at .54. This suggests that synchronized squawks play an important role in establishing physical synchrony. The probability of a squawk bout becoming a synchronized squawk was .29. This raises the question of what specifically makes some squawks become synchronous and others not.

There was no significant difference in the duration of squawk bouts that became synchronous (M = 13.83 s, SD = 10.57) and squawk bouts that did not become synchronous (M = 14.20 s, SD = 28.70), $t(96) = -.069$, $p > .05$. This suggests that the duration of squawk bouts is not related to whether or not the squawks become synchronized.

Table 4 presents the number of occurrences of pursuit, contact, and display behaviors during a squawk bout that became vocally synchronized with and without physical synchrony. There was no significant difference in pursuit behaviors during squawk bouts that became synchronous accompanied with physical synchrony (N = 9) and squawk bouts that became synchronous without physical synchrony (N = 4, refer to Table 5 for the Binomial Sign test p-values for this section). While differences for display behaviors were not significant, display behaviors occurred more frequently during the squawks that became synchronous with physical synchrony (N = 9) than without physical synchrony (N = 2). Contact behaviors occurred significantly more during the squawk bouts that became synchronous with physical synchrony (N = 7) than without physical synchrony (N = 0). When combining the three classes, there were significantly more squawk bouts that became synchronous with physical synchrony (N = 25) than without physical synchrony (N = 6). There were significantly more behavioral classes observed in squawk bouts that become synchronous with physical synchrony than squawk bouts that become synchronous without physical synchrony.

Table 5 The number of occurrences of pursuit, contact, and display behaviors during a squawk bout that becomes vocally synchronized with and without physical synchrony and the corresponding two-tailed p-values. Significance is indicated by an asterisk

Behavioral Classes	With Physical Synchrony	Without Physical Synchrony	*P-Values*
Pursuit			
Total Pursuit	9	4	.2668
Display			
Total Display	9	2	.0654
Contact			
Total Contact	7	0	.0156*
Total Behaviors	25	6	.0008*

Discussion

We examined the frequency and characteristics of behavioral events, classes, and vocalizations during aggressive encounters between Atlantic spotted dolphins and bottlenose dolphins that contained synchrony. Our study indicated that synchrony was associated with a heightened state of aggression containing a high frequency of aggressive behavioral events. The results revealed that there are clear behavioral classes that occur more frequently during aggressive synchronous bouts than during aggressive nonsynchrony. When proportionate to time, the rate per minute of pursuit and contact behaviors were significantly higher during aggressive synchrony than during aggression without synchrony. Although the rate per minute of display behaviors was not significantly different, the magnitude between synchronous and nonsynchronous bouts was similar to pursuit and contact behaviors. These results suggest that during synchronous aggression, there is a higher frequency of aggressive contact, pursuit, and display behaviors. Concurrent with Cusick and Herzing's (2014) findings, contact and pursuit behaviors were most frequently observed during escalated aggression as they may cause the most bodily harm to the receiver. Displays were also important, possibly functioning as an aggressive threat (Cusick and Herzing 2014).

If groups of dolphins were large (i.e., 11 individuals or more), they tended to remain synchronous for a longer duration than if they were smaller (i.e., 10 or fewer). However, smaller groups of dolphins became synchronous more frequently. Previous research has suggested that it takes up to six spotted dolphins to overcome a single bottlenose dolphin (Herzing and Johnson 2015). As the group size of the dolphins increased, so did the duration of the synchronous event. The larger groups may remain synchronous for a longer period because of the increased hydrodynamic advantage gained from synchronous swimming (Fellner et al. 2012). Additionally, because of the size discrepancy between these two sympatric species, spotted dolphins may need different strategies as the larger species or animal are typically considered dominant (Arnott and Elwood 2009). The duration of the synchronous event as a function of group size may be a strategy the smaller spotted dolphins use during interspecies aggression.

There was also a higher frequency of behavioral classes observed during synchrony in smaller groups of dolphins than in larger groups of dolphins, suggesting that synchrony alone in large groups may serve as an aggressive display, and other aggressive behavioral events are not needed as much for a dynamic shift to occur in their favor when fighting with bottlenose dolphins. However, if the group is smaller, the dolphins may need additional aggressive behaviors for a dynamic shift to occur in their favor. Another possibility for the difference in frequency of behavioral classes exhibited by the different group sizes is that the dolphins are assessing their options in the aggressive encounter. For example, black-chinned hummingbirds (*Archilochus alexandri*) have been seen to accurately assess the fighting ability of their opponents along with the value of the contested resources (Ewald 1985). Thrips (*Elaphrothrips tuberculatus*) have also been found to adjust their fighting tactics based on the size of the other male. Specifically, smaller males will flip, a defensive maneuver to avoid stabbing from the other male (Crespi 1986). Fighting is costly in terms of energy use and risk of injury, thus making it beneficial for gaining of information regarding the situation to aid the animal in making an appropriate tactical decision. The spotted dolphins may be assessing themselves, their group size, and their opponents, adjusting their tactics appropriately, similar to what hummingbirds and thrips do. If the dolphins assess that their group size is small during this aggressive encounter, the present results suggest that they adjust their tactics by increasing the amount of aggressive behaviors exhibited. Spotted dolphins have been seen to adjust their aggressive behaviors based on group composition. Spotted dolphins will exhibit more biting, chasing, and contact behaviors during interspecific aggression and use more display behaviors during intraspecific aggression (Volker 2016). When fighting intraspecifically, they use less risky and energy intensive behaviors than when fighting interspecifically (Volker 2016). This suggests that individuals in this population of spotted dolphins are evaluating the aggressive encounter and adjusting their tactics accordingly, whether it is adjusting based on species and/or group size.

When pursuit, contact, and display behavioral classes were combined, there were significantly more aggressive behavioral events during synchrony per dolphin than immediately before and after synchrony. While not significant, the results were trending towards a greater number of behaviors before synchrony than after synchrony. However, it is reasonable to predict that there are more behavioral events before and during synchrony than after synchrony as the aggressive encounter is likely resolved. Despite group size, the behavioral classes (contact, pursuit, and display) that were observed preceding synchrony, during synchrony, and after synchrony had ended tended to follow a similar pattern, with behavioral classes observed being high immediately before synchrony, escalating further during synchrony, and substantially decreasing after synchrony had ended. This indicates that the synchronous state may be the heightened peak of spotted dolphin aggression containing a high frequency of aggressive behavioral events. Aggression then appears to be resolved after synchrony is disengaged. Many species engage in threat displays preceding the heightened peak of the aggression. Male mountain gorillas (*Gorilla beringei*) when encountering another group engage in chest banging and charging, but contact aggression is low unless there are a high number of potential migrants (Sicotte 1993). Marine iguanas (*Amblyrhynchus cristatus*) also demonstrate a threat display, followed by a heightened state of contact aggression if the opponent demonstrates the same threat display, with the aggression ending when one gives up or the rival is pushed off the rock signaling a drastic decrease in aggressive behaviors (Eibl-Eibesfeldt 1966). As threats escalate, a heightened state of aggression occurs, with a drastic decrease in behaviors after the aggression has resolved. In spotted dolphins, aggressive behaviors begin to escalate just before synchrony with synchrony being the heightened state of aggression that also occurs in some intergroup mountain gorilla fights and marine iguana fights.

Also occurring with the beginning of synchrony at a very high probability were synchronized squawk bouts. In addition, synchronized squawk bouts had a high probability of ending with the end of physical synchrony. Due to the high probability of this co-occurrence, this suggests that synchronized squawk bouts play an important role in the synchronization of physical behaviors. Synchronized squawks may serve as an amplified signal for behavioral coordination (Herzing 2015) with synchrony being a physical summation. In addition, synchronized squawks can act as a powerful signal to deter other attackers or attract other male coalitions (Herzing 2015). The coherent summation of synchronized squawks allows the signal to extend past its normal reach, which would allow for other dolphins, friend or foe, to hear (Herzing 2015). In humans, it has been suggested that music and dance evolved as a coalition signaling system (Hagen and Bryant 2003). An ideal signal of coalition quality is one that indicates the group has internal stability, represents past stability, and has the ability to execute coordinated and complex actions (Hagen and Bryant 2003). Music and dance in humans can function as a credible signal because they require practice and indicate that the coalition members have associated with each other in the past and continue to associate with each other. If it is a new coalition, it is likely that they have had less practice and are only able to perform simple and uncomplicated music and dance. Music and dance have both a synchronized acoustic and physical component similar to the co-occurrence of synchronized squawks and physical synchrony in spotted dolphins. This combination of both synchronized squawks and physical synchrony may be an effective coalition signaling system to the bottlenose dolphins.

There was also a high probability of squawk bouts occurring before synchronized squawk bouts, which indicates that there is a sequence that occurs for squawks to become synchronized. The dolphins begin with disorganized squawks, which then become more coordinated and transform into synchronous squawks. However, the synchronization of squawks did not always occur with physical synchrony. This suggests that there are differences in the squawk bouts that precede synchronized squawks that occur with physical synchrony and the bouts that precede synchronized squawks that do not occur with any physical synchrony. The results revealed that there was no difference in the duration of squawk bouts that preceded synchronized squawks and the squawk bouts that did not occur with synchronized squawks. This suggests that length of time squawking does not affect whether these squawks will become synchronous and occur with physical synchrony. However, absolute power, squawk types, and other aspects were not measured and there may be other differences.

However, the results do indicate that physical behaviors occurring during squawk bouts that precede synchronized squawks may affect whether physical synchrony will occur with these synchronized squawks. The results show that there are significantly more aggressive behaviors when behavioral classes are combined (contact, pursuit, and display behaviors) in squawk bouts that precede synchronized squawk bouts occurring with physical synchrony than squawk bouts that become synchronous not accompanying physical synchrony. This suggests that escalated aggressive behaviors may be needed during squawk bouts that become synchronous to also have physical synchrony. Specifically, the behavioral classes of contact and display behaviors were much higher during these pre-synchronous squawk bouts. This suggests that these may be key behaviors that precede physical synchrony. Neotropical tree frogs also synchronize their vocalizations during aggression, although they synchronize their calls with that of another intruding male in order to minimize acoustic interference in a noisy environment (Narins 1983). The synchronous vocalizations of the dolphins may also serve a similar purpose for communication during aggression or may create a more powerful signal with physical synchrony during aggression. Additionally, chimpanzees engage in pant hoot chorusing; while not a synchronous vocalization, it is a vocal interaction that can indicate affiliative relationships between males engaged in the pant hoot. Chimpanzees are more likely to participate in a pant hoot chorus with preferred long-term social partners, however, it can also demonstrate short-term affiliations between males (Fedurek et al. 2013). Synchronized squawks in spotted dolphins may serve a similar function, demonstrating both long-term affiliations of established coalitions and the short-term affiliation of several established coalitions to form a super-coalition, which often happens during aggression in this population of dolphins (Herzing and Johnson 2015).

The results of this study are the first to describe and analyze not only physical synchrony but also acoustic synchrony during aggression underwater with a population of wild dolphins. These results provide an important look at synchrony in this species in a unique underwater environment. Synchrony was demonstrated by Cusick and Herzing (2014) to have a profound impact on the outcome of a dynamic shift during interspecies aggression. The current study further analyzed this important function of wild Atlantic spotted dolphin behavior. The results of this study allow us to understand the dynamics of adult synchrony underwater during aggression. The most frequent behaviors and vocalizations occurring with synchronous aggression have been determined in this study. In addition, insight has been gained on the process of synchrony.

What is not known from this study is the process by which these dolphins develop the skill to synchronize physically and vocally. Future research should analyze how juvenile dolphins develop this crucial skill. Male adult dolphins use synchrony during interspecies aggression as a valuable tool in gaining the upper hand against the physically much larger bottlenose dolphins. The role of alliances and coalitions developed during the juvenile period and subsequent synchronous abilities would also be valuable in understanding if there is a social developmental aspect in learning this important skill. This study has established a baseline of behavioral events, classes, and vocalizations that occur with synchrony making this a valuable study for future research of synchrony in dolphins.

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