



Thunks: Evidence for Varied Harmonic Structure in an Atlantic Bottlenose Dolphin (*Tursiops truncatus*) Sound

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McCowan and Reiss first reported the “thunk” sound of the Atlantic bottlenose dolphin (*Tursiops truncatus*) during separations and discipline behavior of mother-calf dyads. However, since this initial report, no other studies have thoroughly investigated this sound. A bottlenose dolphin mother and calf were observed during the first 30 days of life. Thunk production during separations within the mother-calf dyad and discipline behavioral events were analyzed, as thunks were predominately produced in these contexts during the original report by McCowan and Reiss. We found that variation occurs within the thunk sound, contrary to how this acoustic signal has been previously defined. We report the presence of two different types of thunks primarily present in separation events during the calf’s early life: the low harmonic range (LHR) and high harmonic range (HHR) thunk. LHR and HHR thunks varied in harmonic structure, but did not have significantly different peak frequencies. Furthermore, in order to determine the salience of the thunk sound to separation and discipline events, we also report on the presence of burst pulses and signature whistles when compared to thunk production. Thunks were the most produced sound during separation events, while burst pulses were more common during the mother’s discipline of the calf. The mother’s signature whistle was not as common during the course of the study, suggesting that, at least within this bottlenose dolphin mother-calf dyad, other sounds were more important for dyad communication within separation and discipline events.

Thunks are a low frequency sound that are reportedly used by bottlenose dolphin mothers (*Tursiops truncatus*) in soliciting reunions with their calves (McCowan & Reiss, 1995). The acoustic structure of the thunk sound has previously been described as a wideband, low frequency sound that appears to be somewhat stereotyped. Despite the presence of the thunk in at least one social group of bottlenose dolphins, no other studies have sought to investigate this signal further. Instead, more is known regarding the “pop” vocalization, which appears somewhat contextually similar to the thunk.

Pops are also a low frequency signal, attributed to bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia (Connor & Smolker, 1996; Vollmer, Hayek, Heithaus, & Connor, 2015). Male dolphins in Shark Bay emit pops when soliciting a female consort to return to a male alliance, and there is some evidence that Shark Bay mothers use this sound to prompt the return of their calves after a separation (Connor & Smolker, 1996). Given the similarity in contextual usage of these two sounds, McCowan and Reiss (1995) argued that the structural differences between pops and thunks (i.e., thunks are longer in duration and have lower peak and maximum frequencies) may be due to inter-population differences. McCowan and Reiss (1995) also suggested that differences between pops and thunks could be sex-based as they reported that, while the females in their study were responsible for thunk production, the males produced pops. However, despite these speculations, parameters of the pops mentioned in the original thunk study were not reported, so the variation between the female-produced thunks and the male-produced pops cannot be fully understood.

Furthermore, if similarities do exist between the pops produced in Shark Bay and the pops produced by dolphins in McCowan and Reiss (1995), they cannot be identified.

Other research has failed to find that pops exist across the *Tursiops* genus (see Appendix in Vollmer et al., 2015). Thus, the pops produced by the male dolphins in McCowan and Reiss's (1995) study may not have been equivalent to the pops in Connor and Smolker's population, but may have been higher frequency variations of the thunk sound.

Based on McCowan and Reiss's work, thunks have a peak frequency between 0.27–0.35 kHz, with harmonic structures between 0.13–5.56 kHz. However, it is possible that thunks have more variability in their structure, with a greater range in harmonic frequency than has been previously reported. It is not unusual for dolphin sounds to contain an element of variability. For example, burst pulse sounds, a purportedly aggressive sound produced by bottlenose dolphins (Overstrom, 1983), fall along a continuum based on the sounds' pulse repetition rate or number of pulses per second (Blomqvist & Amundin, 2004). Dolphin whistles can also vary with alterations in frequency and amplitude modulation. Some whistles contain pulsed qualities (Lammers, Au, & Herzog, 2003), and may exist as an intermediary between pure tones and burst pulses (Lammers & Oswald, 2015). Thus, dolphin vocalizations often do not fall into discrete categories.

Here we report on thunk production within a mother-calf dyad, housed at the same facility as the animals in the original thunk study conducted by McCowan and Reiss (1995). We analyzed thunks in similar contexts as the original study (i.e., separation and discipline events), and hypothesized that the parameters of the thunks identified in these contexts would reflect variation in the sound. Additionally, we investigated the contextual value of thunks by comparing the production of this sound to periods when the mother and calf were pair swimming, as well as comparing this sound to the production of other sounds that may be relevant in mother-calf communication. We hypothesized that thunks would be contextually salient to the reunion of a mother-calf dyad.

Method

Study Animals and Facility

Data were collected from bottlenose dolphins at the same facility studied by McCowan and Reiss (1995) so we would have access to the female social group originally reported to produce thunks. Data were collected opportunistically between January 10th, 2014 and February 7th, 2014 from the Marine Research Center (MRC) habitat at Six Flags Discovery Kingdom (Vallejo, CA) as part of a larger, concurrent study on whistle use within this social group (Ames, 2016). The Institutional Animal Care and Use Committees (IACUC) approval was obtained for the completion of this study through The University of Southern Mississippi. Six Flags Discovery Kingdom is an AZA accredited facility that meets U.S. regulations regarding the care of the animals.

All of the bottlenose dolphins in the current study were female, eliminating the possibility that variations in the thunk sound were sex-based. The subjects of this study were a primiparous 9-year-old mother (BEL) and her calf (MIR) born January 9, 2014. Additional group members consisted of five other adult females (CHE, JAS, MAT, YOS, and PIN). CHE was one of the original dolphins reported to make this sound in McCowan and Reiss's (1995) study, and is the mother of BEL.

Materials

A CR-1 hydrophone (Cetacean Research Technology, Seattle, WA) was placed in an acoustically transparent cylindrical tube adjacent to the viewing window of MRC's center pool (Figure 1). Vocalizations detected by the hydrophone (linear frequency range: 0.16 Hz–48 kHz +/- 3 dB) were recorded by a Sony Audio Recorder PCM-M10 (frequency response: 20 Hz–40 kHz at 96 kHz sampling rate). However, the PCM-M10 audio recordings were limited to a frequency response of 20 Hz–20 kHz (44.1 kHz sampling rate) when

the sound was input through a wide-angle lens Canon Vixia HF200 used for behavioral observations. Inputting sound through the Vixia HF200 allowed for under water recordings to sync with behaviors recorded by the camera. The camera was placed in front of the observational window of the habitat's center pool during recording sessions. Recordings occurred opportunistically throughout the day, almost daily through the course of the study.

Discovery Kingdom MRC

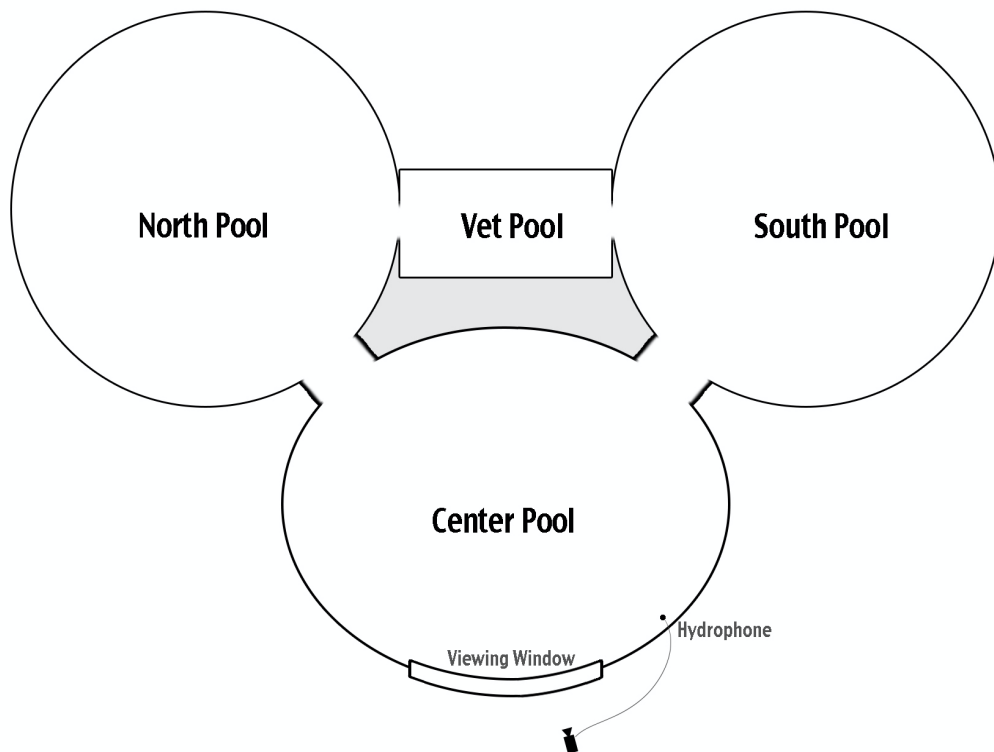


Figure 1. MRC habitat at Six Flags Discovery Kingdom accompanied by placement of video camera and hydrophone recording device (adapted from Ames, 2016).

Equipment used in McCowan and Reiss's (1995) original study consisted of an Akai 2600 tape recorder (flat frequency response from 30 Hz–22 kHz) or a Sony Beta Hi-fi video recorder (flat frequency response from 30 Hz–25 kHz) with a Finley-Hill EM 8 hydrophone (flat frequency response from 30 Hz–28 kHz). Thus the frequency response upper and lower limits of the equipment in the current study were less than that of the recording equipment in the previous report.

The center pool was an oval pool 43 feet wide, 60 feet long and 15 feet in depth. The adjacent pools were cylindrical pools 50 feet in diameter and 15 feet in depth. Each pool could be closed off from the others via a gating system.

When the mother-calf dyad was physically separated from other group members, sounds they produced were still detectable as the gates separating the pools were not acoustically opaque. For the majority of the calf's first month of life, the dyad was physically isolated in the center pool (with the hydrophone closer to the dyad than the other group members). Data in which one or more remaining group members were also in the center pool with the dyad were excluded from this study. Only data during which the dyad was physically isolated were analyzed. We chose this data as a means of limiting potential thunks that could have been produced by other animals during calf interactions, as well as ensuring the mother and calf were the closest animals in proximity to the hydrophone during the study. However, this still does not eliminate the potential that other animals produced thunks recorded by the hydrophone. Subsequently, the value of the results reported here will pertain to the entire female social group, as females have not yet been shown to produce higher frequency thunks in the literature. If variation within the thunk sound was due to the sound's production by other females, then sex-based explanations for variations in the call can be eliminated. Additionally, we noted if BEL produced a bubble stream coinciding with the appearance of a thunk in the data set, as this increased the probability that she was the signaling animal.

Procedure

Behavioral analysis. One month of data (30 days) were collected over the course of the study. We were most interested in analyzing the first 30 days of the calf's life, as this period would more likely contain separations that were not tolerated by the mother (Mann & Smuts, 1998), and might therefore provide the most substantial sample of thunks. The 30 days during which data were collected were segmented into 10-day blocks for the investigation of thunk production over time.

McCowan and Reiss (1995) originally chose to look at 10-s time intervals surrounding the thunks in order to determine the contextual properties of the sound. We did not choose to employ this method because we wanted to investigate the sound's variation and salience to the contexts in which it has already been associated (i.e., separation and discipline behaviors). Therefore, video data collected when the mother and calf were isolated in the center pool were observed for the occurrence of separation and discipline behaviors (see Table 1 for ethogram). A total of 1,779 min (593 min from each 10-day period) of video data were observed. We chose 593 min as the amount of data selected from each period because this was the total amount of video data available during the time period with the smallest sample, the third 10-day time block. During the third time block, there was increasing presence of additional group members in the center pool, so the amount of data collected when the mother and calf were physically isolated was more limited.

In the current study, each occurrence of a separation or discipline behavior was considered to be an "event". Sounds were quantified within an event's duration (e.g., if $n = 5$ thunks for an event, then five thunks occurred between the start and end of the event). The duration of an event began or ended in one of the following ways:

- 1) Both BEL and MIR were on screen when discipline or separation events began or ended. An event's duration began at the start of calf discipline, or if a clear separation within the dyad was apparent (i.e., distance existed between the mother and calf and/or the mother or calf altered swim pattern without a co-occurring change by the other animal). An event was considered over with the calf's return to either echelon position or mother-calf position.
- 2) Both BEL and MIR entered or left the visible area while still engaged in a discipline or separation event (events did not begin or continue if both animals were off-screen, as it was not possible to determine the dyad's behaviors out of sight).
- 3) BEL or MIR entered or departed the screen individually (i.e., without the other animal on screen). We considered events where only one animal was on screen as "other" events because the physical distance between the dyad was unclear.

We used an all occurrence sampling method for inclusion of all events that occurred within the data set for analyses ($n = 461$ total events).

Table 1
Ethogram of Study Events and Behaviors

Event Type	Behavior	Operational Definition
Discipline		Mother disciplines calf with one of the below behaviors.
	Chase	Mom quickly swims after calf as calf attempts to separate or flee the dyad.
	Push to surface	Mom pushes calf with rostrum to surface.
	Push to bottom	Mom pushes calf to bottom of the pool with rostrum.
	Push to wall	Mom pushes calf to wall with rostrum.
	Push	Mom pushes calf in some other way unspecified.
	Beach	Mom is holding calf at surface, effectively beaching her in some way other than using her rostrum (e.g., melon, dorsal, ventral etc.).
Separations < 2 m	Separation of less than two meters	Calf or mother has separated from the dyad, but the distance is not greater than two meters. The calf is not in a protected position (e.g., echelon or mother-calf swimming).
Separations > 2 m	Separation of more than two meters	Calf and/or mother has separated from the dyad at a distance greater than two meters.
Pair Swim		Mother and calf movements are continuously synchronized. The calf is generally in a protected position (e.g., echelon or mother-calf swimming) or is swimming beside the mother in close proximity.
	Echelon position	Mother and calf swim very close together. The calf's head is next to the mother's fin and body slightly above the mother, touching or nearly touching the mother's body.
	Mother-calf position	Calf swims under the mother, its head touching or near touching her mammary region.
Other		Separation events that cannot be classified according to distance. Either the calf or mother is on camera, so separation is visible, but other animal is off camera.

As a behavioral control, we compared thunk totals in separation and discipline events with data during which the dyad was pair swimming with the calf in close proximity (Table 1). A total duration of 68 min of pair swimming were randomly selected from time in videos where discipline or separation behaviors were not present. We chose to sample 68 min as this was the total amount of time across all 461 of the behavioral events. Sounds were then coded during these minutes and later compared statistically to sounds produced during discipline and separation events.

Finally, we wanted to eliminate the possibility that variations in the thunk sound were due to the orientation of BEL to the hydrophone, as the harmonic structures of cetacean sounds may vary depending on whether an animal is facing the hydrophone

(Lammers & Au, 2003; Miller, 2002). Orientation was classified as “towards” the hydrophone when the mother’s melon faced the hydrophone within an estimated 0–45 degree angle (Branstetter, Black, & Bakhtiari, 2013).

Acoustic analysis. Raven Pro 1.4 (Cornell University) was used for sound analysis. Sounds were totaled over the duration of the event identified using a Hann window size of 512 (512 DFT) with 50% overlap and 256 hop size. Thunks produced in the dataset during periods when the dyad was not on camera were not analyzed.

We identified two primary thunk types: LHR (low harmonic range) and HHR (high harmonic range) thunks. Types were categorized by human judges (see Statistical Analysis below) based on differences in the harmonic structures of the sound on spectrograms (Figure 2). LHR sounds had fewer harmonics in the sound with the highest spectrographically visible harmonic generally around 5 kHz based on parameters reported by McCowan and Reiss (1995). HHR thunks consisted of an increased number of harmonics with the highest harmonics often nearing the ultrasonic range. Parameters used to compare the two thunk sound types included the minimum, maximum, and peak frequencies, as well as the frequency range and sound duration. We chose these parameters based on what was reported in the original thunk study. Parameters were extracted using Raven Pro 1.4 for all occurrences of HHR thunks ($n = 88$). LHR thunks were randomly sampled due to the higher presence of these sounds in the data ($n = 405$). Parameters sampled from LHR thunks were then compared to parameters extracted from the HHR thunks.

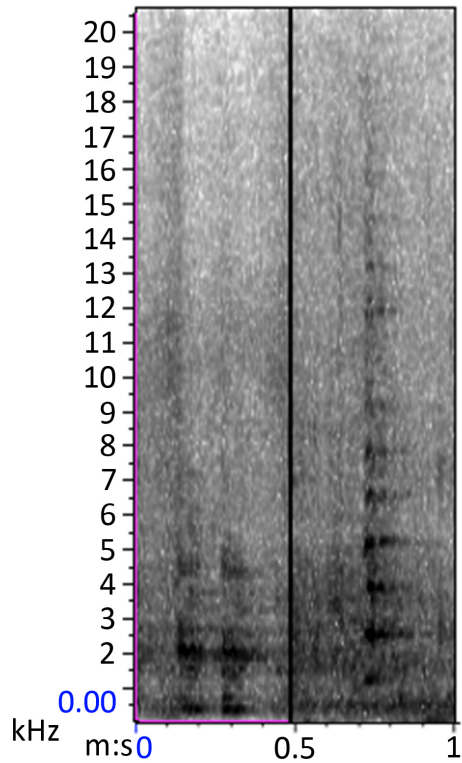


Figure 2. Representations of LHR (left) and HHR (right) thunks. X-axis is based on half-second intervals.

Two other sound types were analyzed in order to determine the salience of these sounds during separation and discipline events when compared to thunks: the signature whistle of BEL (adapted from Ames, 2016) and burst pulses (Figure 3). Signature whistles are narrow band tonal sounds, which may facilitate reunions after mother-calf separations (McBride & Kritzler, 1951; Mello & Amundin, 2005; Smolker, Mann, & Smuts, 1993). Burst pulses have previously been identified during aggressive contexts in

bottlenose dolphins (Blomqvist & Amundin, 2004; Overstrom, 1983). Therefore, both sounds were suspected to appear during the current study.

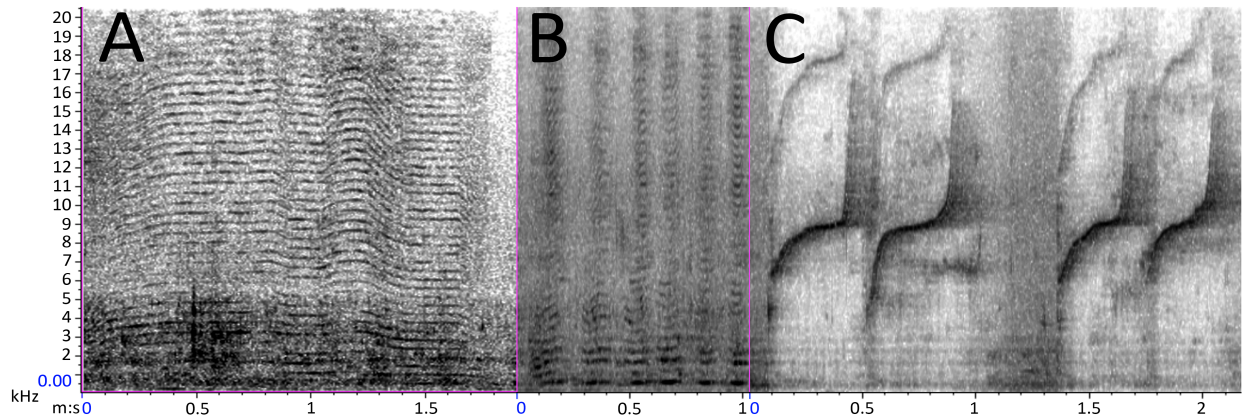


Figure 3. Additional sound types: (A) burst pulse > 1 s, (B) burst pulse < 1 s, and (C) BEL’s signature whistle. X-axis is based on half-second intervals.

Burst pulses are characterized by clicks that occur in rapid succession, often appearing as having indistinguishable inter-click intervals on a spectrogram. This sound is sometimes lumped into a broad category within the literature (e.g., Lammers, Schotten, & Au, 2006; Overstrom, 1983), although there is variation in this sound type as well (e.g., pulse-repetition rate, Blomqvist & Amundin, 2004). Here, burst pulses were segmented into two sub-categories: burst pulses with < 1 s duration and burst pulses with > 1 s duration. We chose to look at duration of the sound instead of pulse repetition rate because we also wanted to investigate the possibility that shorter duration pulsed sounds functioned as solicitation calls.

Statistical Analysis

Human judges were used to identify the sounds present during events, as human ratings have shown to be a successful measure in quantifying sounds (Janik, 1999; Sayigh, Esch, Wells, & Janik, 2007). Raters independently identified sound types in 20% of the total video time, which was randomly sampled from the dataset. Inter-rater reliability had to meet 80% agreement on each sound type. Raters agreed 99.7% on thunk identification, 95.5% on short burst pulse identification, 82.7% on long burst pulse identification, and 97.4% regarding BEL’s signature whistles.

We first assessed the prevalence of thunks across event types. Addressing similarities or differences in thunk production between contexts determined if the sound was more salient in some contexts over others. Because group variance was unequal, a Brown-Forsythe ANOVA in congruence with Games-Howell post hoc pairwise comparisons were chosen to test thunk production differences across event types. In order to account for differences in event duration, all sound totals were divided by the number of seconds in each event. We then used the sounds per second values for all events to compare sound production across event types (i.e., comparing separations of < 2 m and > 2 m, discipline, and pair swim states). When thunks were compared across event types, we included all events (i.e., with and without thunk production) so as not to bias the results and to reduce variation in sample sizes obtained from occurrences of events. We repeated this analytical procedure when determining how thunk production changed over the calf’s first month of life (i.e., comparing the three 10-day time periods), and in the comparison of thunk prevalence versus other sound types within and between behavioral events.

T-tests were appropriate to assess if there was any significant difference between the parameters of the LHR and HHR sounds because we had two parameter groups and equal sample sizes. We reported the *t* statistic accordingly if the assumption of homogeneity of variance was violated, Levene’s test: $p < 0.05$. We also used a discriminant function analysis (DFA) to assess the veracity of the raters’ classification of thunk types.

When testing the mother’s orientation to the hydrophone, we treated the data categorically as a simple yes/no paradigm depending on the mother’s melon angle in conjunction with the hydrophone. If the mother’s melon was directed towards the hydrophone within 0–45 degrees during the occurrence of a thunk, this was considered a “yes” in orientation towards the hydrophone. Sum totals of call types were used to weight the categorical input (i.e., if the mother was orienting towards the hydrophone during 231 thunks, the yes category would be weighted by 231). We then used a Fisher’s exact test to compare the two categorical groups. A Fisher’s exact test was also used when we compared thunk type and calf response. Calf response was judged as compliant (i.e., “yes”) if the calf attempted to return or returned to the dyad, and non-compliant (i.e., “no”) if the calf ignored the call or fled from the mother.

Results

A total of 461 events occurred within our data set (Table 2). The majority of events (84.38%) occurred without thunk production. Out of all the events with thunk production ($n = 72$), discipline ($n = 5$, 6.94%) and other ($n = 4$, 5.56%) events were rare, while separation events were more common (separations of < 2 m: $n = 34$, 47.22%; separations of > 2 m: $n = 29$, 40.28%). All discipline events with thunk production ($n = 5$) occurred immediately after separation events (three discipline events occurred immediately after a separation event also including thunks). However, a much higher percentage (92.06%) of separation events with thunk production ($n = 58$) occurred without subsequent discipline. This finding was surprising as McCowan and Reiss (1995) reported significant levels of thunk production when mothers disciplined their calves given a separation of > 5 ft. It was possible that MIR quickly returned to the dyad when thunk production occurred, so that discipline was not necessary within this dyad. However, upon preliminary analyses of calf response to thunk production, we found that the calf was just as likely to comply as she was to not comply with production of either thunk type, $p = 0.168$, two-tailed Fisher’s exact test.

Table 2
Total Event Count and Percentage of Separation and Discipline Events

Event Type	With Thunks	%	Without Thunks	%	Total	First 10 Days	Second 10 Days	Third 10 Days
Separations < 2 m	34	18.68	148	81.32	182	33	56	93
Separations > 2 m	29	15.26	161	84.74	190	32	62	96
Discipline	5	9.26	49	90.74	54	10	28	16
Other	4	12.12	29	87.88	33	10	3	20
Total	72	15.62	389	84.38	461	85	149	225

We observed BEL’s simultaneous bubble stream emission with 41% ($n = 202$) of produced thunks compared to only 18% ($n = 91$) of thunks produced with no bubble stream (bubble stream production was not able to be confirmed or denied for the remaining 41% of thunks). Thus, it was likely that at least 41% of thunks produced in the data set belonged to BEL.

Thunks

Across event types, Brown-Forsythe: $F(3, 347.54) = 4.17, p = 0.006$, total thunk production was significantly higher during separations of < 2 m when compared to discipline and pair swim contexts (see Table 3 for descriptive statistics and pairwise comparisons). However, separation contexts were not significantly different. Additionally, thunk production during separations of > 2 m was significantly more common when compared to pair swimming, but total thunk rate did not differ significantly in discipline and pair swim behaviors (Figure 4).

Table 3
Total Thunk Production Across Events

Event Type	<i>M</i>	<i>SE</i>	Separations < 2 m	Separations > 2 m	Discipline	Pair Swim
Separations < 2 m	0.19	0.05	*	$p = 0.468$	$p = 0.021$	$p = 0.001$
Separations > 2 m	0.11	0.03	$p = 0.468$	*	$p = 0.282$	$p = 0.006$
Discipline	0.04	0.02	$p = 0.021$	$p = 0.282$	*	$p = 0.267$
Pair Swim	0.004	0.004	$p = 0.001$	$p = 0.006$	$p = 0.267$	*

Note. Pairwise comparisons.

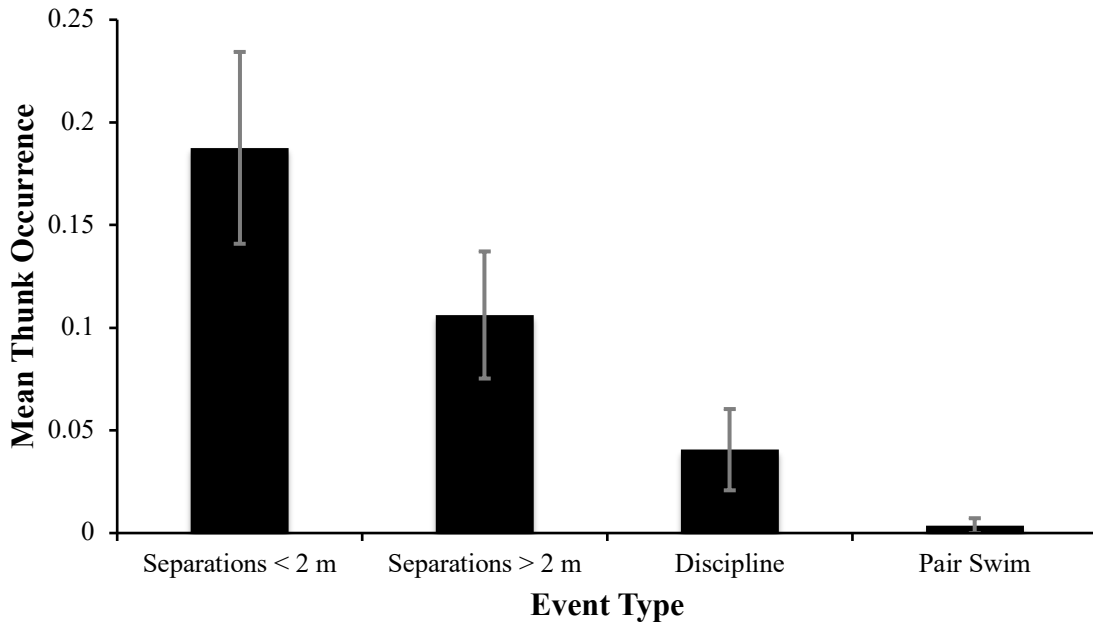


Figure 4. Total thunk production between event types. Error bars represent standard error values.

Variation within the thunk sound. As previously mentioned, we were able to identify two groups of thunks: LHR (low harmonic range) and HHR (high harmonic range). We found significant variation across parameter comparisons, except in peak frequency, $t(139.24) = -0.623$, $p = 0.533$. Thus, peak frequency remained consistent while the other parameters varied. As expected, maximum frequency, $t(95.86) = -12.11$, $p < 0.001$, and frequency range, $t(99.12) = -11.86$, $p < 0.001$, were significantly higher for HHR thunks. The minimum frequency, $t(174) = -3.223$, $p = 0.002$, and duration, $t(174) = -2.129$, $p = 0.035$, were also significantly higher for HHR thunks. A DFA revealed that 87.5% of thunk sounds were correctly classified by the human raters. See Table 4 for parameter descriptive statistics.

Table 4
Descriptive Statistics of LHR and HHR Thunk Duration (s) and Frequency (kHz) Parameters

Thunk	Parameter	<i>M</i>	<i>SE</i>	Min ^b	Max ^b
LHR					
	Minimum frequency ^a	0.54	0.05	0.14	1.84
	Maximum frequency ^a	5.45	0.11	2.95	8.25
	Frequency range	4.91	0.12	1.91	7.51
	Peak frequency	1.55	0.07	0.28	3.94
	Duration	0.09	0.004	0.03	0.30
HHR					
	Minimum frequency ^a	0.76	0.05	0.16	2.22
	Maximum frequency ^a	11.46	0.48	1.67	20.43
	Frequency range	10.70	0.47	1.22	19.80
	Peak frequency	1.64	0.12	0.38	8.81
	Duration	0.11	0.003	0.05	0.22

Note. ^aThe minimum and maximum mean frequencies for LHR and HHR thunks. ^bThe lowest and highest value of each parameter from thunks sampled.

It was imperative to determine if harmonic structures of LHR and HHR thunks varied based on BEL’s position in the pool (e.g., BEL’s orientation towards the hydrophone). There was no significant difference between LHR and HHR thunk production in relationship to the mother’s orientation to the hydrophone, $p = .129$, two-tailed Fisher’s exact test, indicating that the harmonic differences in these sounds were not likely due to the mother facing the hydrophone within a 45-degree angle.

Over the course of the study, the LHR thunk total was significantly higher than the HHR thunk total, $t(567.46) = 3.24$, $p = 0.001$. When LHR and HHR production were analyzed across 10-day time blocks within the calf’s first 30 days of life, Brown-Forsythe: $F(2, 118.1) = 13.02$, $p < 0.001$, LHR rates significantly decreased between the first and second time blocks and first and third 10-day time blocks (Figure 5). HHR thunk rate did decrease over the course of the calf’s first 30 days of life, though not significantly, Brown-Forsythe: $F(2, 176.51) = 1.83$, $p = 0.164$ (Figure 5).

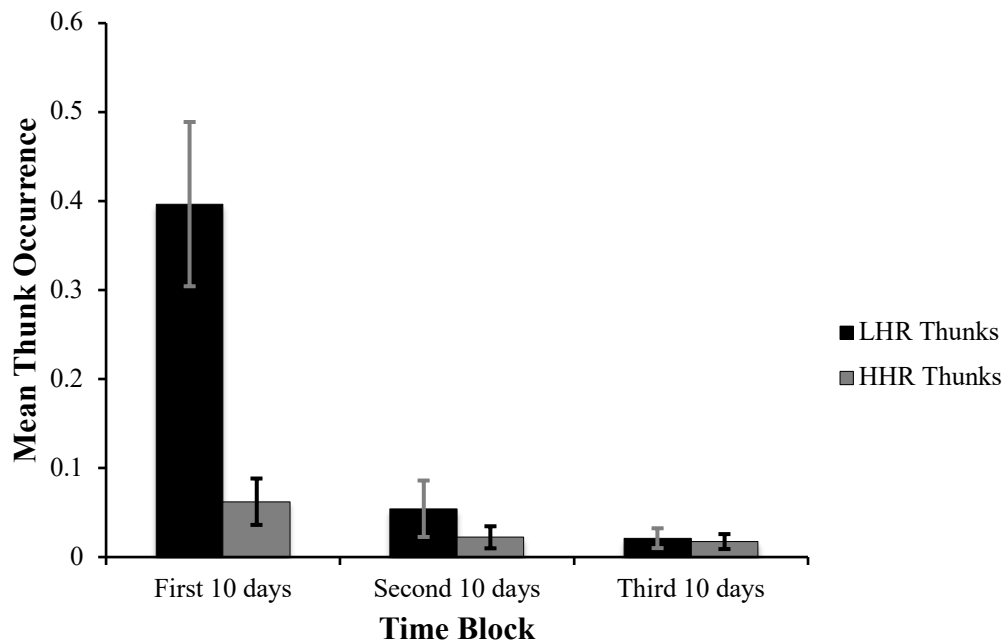


Figure 5. Mean number of LHR and HHR thunks over the first 30 days of life. Error bars represent standard error values.

Salience of Thunks and Other Sounds

Burst pulses < 1 s and thunks were the most commonly produced sound types over the course of the study, Brown-Forsythe: $F(3, 992.97) = 8.79, p < 0.001$. Rates of these sounds were significantly higher than burst pulses > 1 s and signature whistles, but not significantly different from each other. Signature whistles and burst pulses > 1 s were also not significantly different from each other.

During separations of < 2 m, thunks were the most commonly produced sound type when compared to burst pulses with a duration of > 1 s and signature whistles, Brown-Forsythe: $F(3, 384.99) = 5.25, p = 0.001$. Burst pulses with duration of < 1 s were also significantly more common when compared to signature whistles. During separations of > 2 m, thunks were produced significantly more than burst pulses with duration > 1 s, Brown-Forsythe: $F(3, 262.93) = 5.77, p = 0.001$.

Burst pulses were the most common sound type during discipline behaviors, Brown-Forsythe: $F(3, 94.74) = 8.07, p < 0.001$. Specifically, shorter burst pulses occurred more frequently than thunks and the mother's signature whistle, but not significantly more than burst pulses > 1 s long. Burst pulses longer in duration were also significantly different from thunks and signature whistles during discipline events (Figure 6).

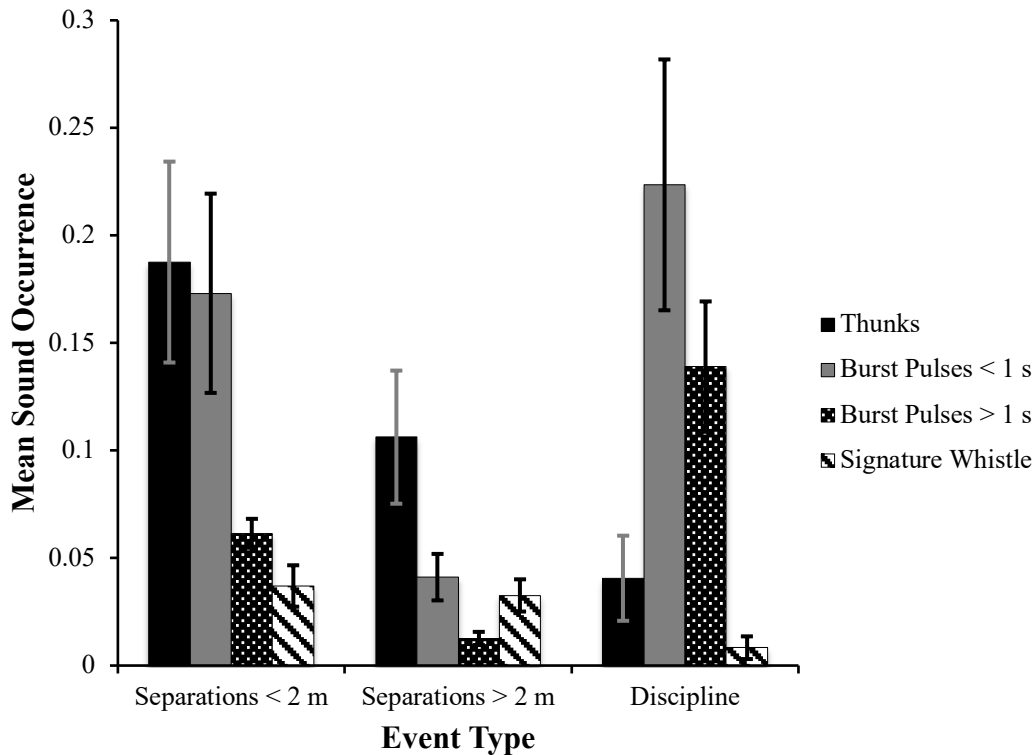


Figure 6. Individual sound types within separation and discipline events. Error bars represent standard error values.

Non-Thunk Events

During events without thunk production, burst pulses < 1 s were produced significantly more than burst pulses > 1 s and signature whistles, Brown-Forsythe: $F(2, 447.94) = 10.69, p < 0.001$ (Table 5). Burst pulses with longer durations were also produced more often than signature whistles. Within separations of < 2 m, signature whistles were produced significantly less than burst pluses < 1 s and burst pulses > 1 s, Brown-Forsythe: $F(2, 163.67) = 6.84, p = 0.011$. Burst pulse types did not significantly differ from each other. Sound types were not significantly different during separations of > 2 m, Brown-Forsythe: $F(2, 385.03) = 2.69, p = 0.069$, and during discipline events, burst pulses > 1 s were significantly more common than signature whistles, Brown-Forsythe: $F(2, 89.17) = 3.14, p = 0.048$ (Figure 7).

Table 5

Production Total, Mean, and Standard Error of Each Sound Within Event Types (With and Without Think Production)

Think Events	Separations < 2 m			Separations > 2 m			Discipline			
	<i>M</i>	<i>SE</i>	Total	<i>M</i>	<i>SE</i>	Total	<i>M</i>	<i>SE</i>	Total	Total
Thunks	0.19	0.05	318	0.11	0.03	148	0.04	0.02	12	478
Burst Pulses										
< 1 s	0.17	0.05	313	0.04	0.01	88	0.22	0.06	71	472
> 1 s	0.06	0.01	169	0.01	0.003	31	0.14	0.03	31	231
Signature whistles	0.04	0.01	26	0.03	0.01	53	0.01	0.01	4	83
Non-Think Events										
Burst Pulses										
< 1 s	0.20	0.06	245	0.03	0.01	63	0.22	0.09	57	365
> 1 s	0.07	0.01	136	0.01	0.003	25	0.09	0.02	30	191
Signature whistles	0.03	0.01	16	0.02	0.01	13	0.03	0.01	3	32

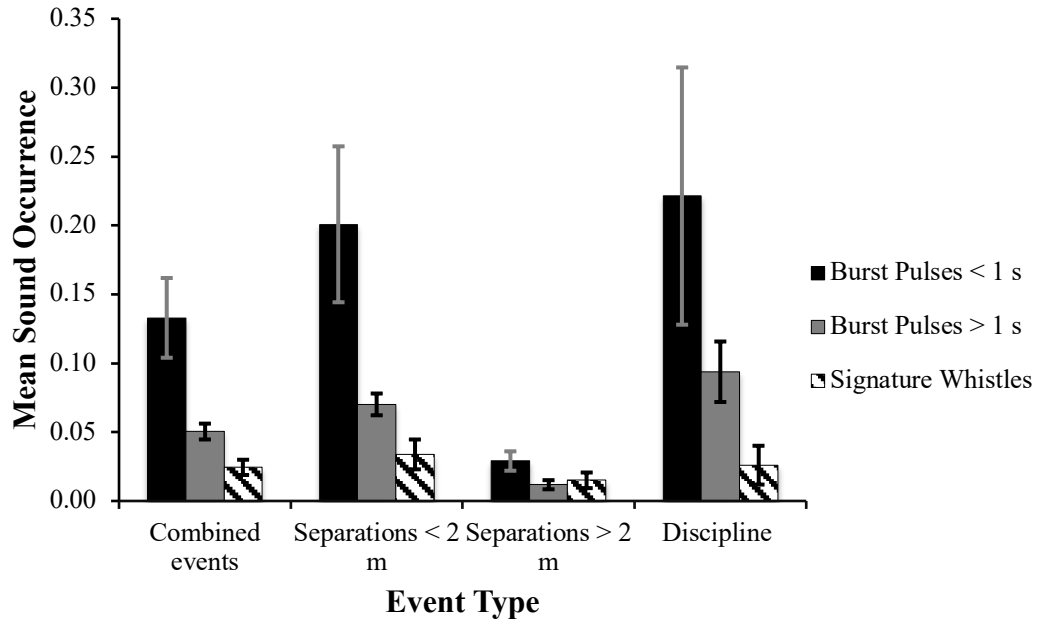


Figure 7. Burst pulses and signature whistles in non-think events and in events combined. Error bars represent standard error values.

Discussion

Variation in the Thunk Sound

Based on the comparisons of the LHR and HHR sound, we are confident that at least two variations within the thunk sound exist: a lower harmonically structured sound, similar to what was first described by McCowan and Reiss (1995), and a higher harmonically structured sound. There was no difference in the peak frequencies of these sounds, but HHR thunks tended to be longer in duration and with higher minimum, maximum, and delta frequencies.

Harmonic structure of dolphin sounds can vary depending on whether an animal is facing towards or away from the recipient of a sound, providing movement cues of the signaling animal (Branstetter, Moore, Finneran, Tormey, & Aihara, 2012; Lammers & Au, 2003; Miller, 2002). Specifically, directional information embedded in harmonic structure may be similar for recipients on a horizontal axis of 0-45 degrees from the signaler. Therefore, we questioned whether the harmonic changes in the thunk sound were used by the mother to indicate her direction of travel to the calf. If the thunk sound did include directional cues, then variation in harmonic structure of this sound should also change based on the mother's orientation to the hydrophone during thunk production (Lammers & Au, 2003; Miller, 2002). We did not find that the parameters of the sound changed based on BEL's orientation to the hydrophone (i.e., < 45 degrees versus > 45 degrees), indicating that the variation in harmonic structure was not due to directionality. Thus, our findings support two variants in the thunk sound.

Variation in signaling may convey the level of arousal of the signaling animal (Murray, Mercado, & Roitblat, 1998; Wilson, 1975). In the case of thunks, because we found that this signal was most common in separation contexts, the variation in the sound type may have been due to the mother's level of threat in recalling her calf. The higher frequency components of the HHR thunk may have been added to the call when the mother's demand for the calf's return to the dyad intensified. When a signaler increases the intensity of a threat, additional components may be added to the signal. For example, rhesus macaques may begin an aggressive display with a stare, but may add open mouth gestures or other facial cues, sounds, and hand slaps to increase the intensity of a threat (Maestripietri, 1997; Wilson, 1975).

Additional signal components may also encode information regarding the urgency of an induced response. For example, white-browed scrubwrens (*Sericornis frontalis*) add sound elements and increase the minimum frequency of alarm calls when the threat of predation is greater (Leavesley & Magrath, 2005). Playbacks indicate that multi-element alarm calls prompt more urgent responses from scrubwrens, including an immediate flee to safety (Leavesley & Magrath, 2005). Likewise, Arabian babblers (*Turdoides squamiceps*) produce a greater number of higher frequency mobbing calls when threat intensity increases (Naguib et al., 1999).

It may be possible that HHR thunks were produced in our study when the mother perceived a greater threat to the calf's safety. This may explain why there was no significant decrease in HHR production over the calf's first month of life. We did see a significant decrease in LHR production over time, however. This trend in LHR calls may be consistent with increased calf independence as calves mature (Mann & Smuts, 1998). Thus, as calf independence becomes tolerated by the mother (Fripp & Tyack, 2008; Mann & Smuts, 1998), less threatening calls (e.g., calls prompting less urgent responses from the calf) may become obsolete, while calls indicating urgency remain.

Salience of Thunks and Other Sounds

Thunks were more common than other sound types during separation events, further supporting this sound as a solicitation call. Signature whistles were the least common sound during shorter distance separations, and were produced less than thunks and burst pulses < 1 s during greater distance separations, although not significantly. Production of the mother's signature whistle in separations of > 2 m complements the understanding that signature whistles are group cohesion calls (Janik & Slater, 1998). However, because they were less common than thunks or short burst pulses, other sounds may be more pertinent to mother-calf communication. Furthermore, calves may be responsible for facilitating reunions of the dyad through their own whistle production (Mello & Amundin, 2005; Smolker et al., 1993), which would also be consistent with why signature whistles were less common in separation contexts here.

As burst pulses are commonly recognized as an aggressive sound (Blomqvist & Amundin, 2004; Overstrom, 1983), it was unexpected to find that burst pulses with shorter durations were also common during separation contexts, including non-thunk events when separations were < 2 m. However, some evidence suggests that burst pulses may be relevant to short distance communication (Lammers et al., 2006; Watkins & Schevill, 1974). Both burst pulse categories were significantly more common than thunks and signature whistles during discipline contexts (including signature whistles in non-thunk events), furthering the aggressive implication of these sounds.

The Original and Current Studies

In congruence with McCowan and Reiss's (1995) hypotheses, we did find that thunks were more prominent in separation contexts. However, the original report indicated that thunks were eight times more likely to occur during separations of > 5 ft (i.e., "departures" according to McCowan and Reiss), while in the current study, thunks were more common in separations of < 2 m. With the original metric for separation distinguished at 5 ft, and the current study's distinguished at 2 m, it is possible that a separation distance exists in the 1 ½ overlap that may satisfy the findings from both studies. However, it is more likely that individual differences in maternal style play a role in the distance a mother allows her calf to stray (Hill, Greer, Solangi, & Kuczaj, 2007). The original study appeared to show variation in thunk production even between pairs (see Table 3 in McCowan & Reiss, 1995), as at least one female (pair 3) had a higher occurrence of separation and discipline events during which thunks did not occur in comparison to events where thunks were produced.

The principal difference between the original and current findings concerned the acoustic structure of thunks. McCowan and Reiss (1995) found that thunk peak frequency was between 0.27–0.35 kHz with a harmonic range of 0.13–5.56 kHz. Some of our sounds met these criteria, with some thunks having extremely low peak frequencies (Figure 8). However, we chose to group our sounds by harmonic structure instead of peak frequency because peak frequency was not significantly different overall. Subsequently, we found that thunk peak frequency was higher than originally reported (0.28–8.81 kHz, Table 4). It is possible that McCowan and Reiss (1995) limited their thunk identification to these very low harmonic sounds, which we included in our LHR category (see LHR thunk, supplementary material). However, given our findings, thunks should include sounds of similar structure with parameters at higher frequencies as well.

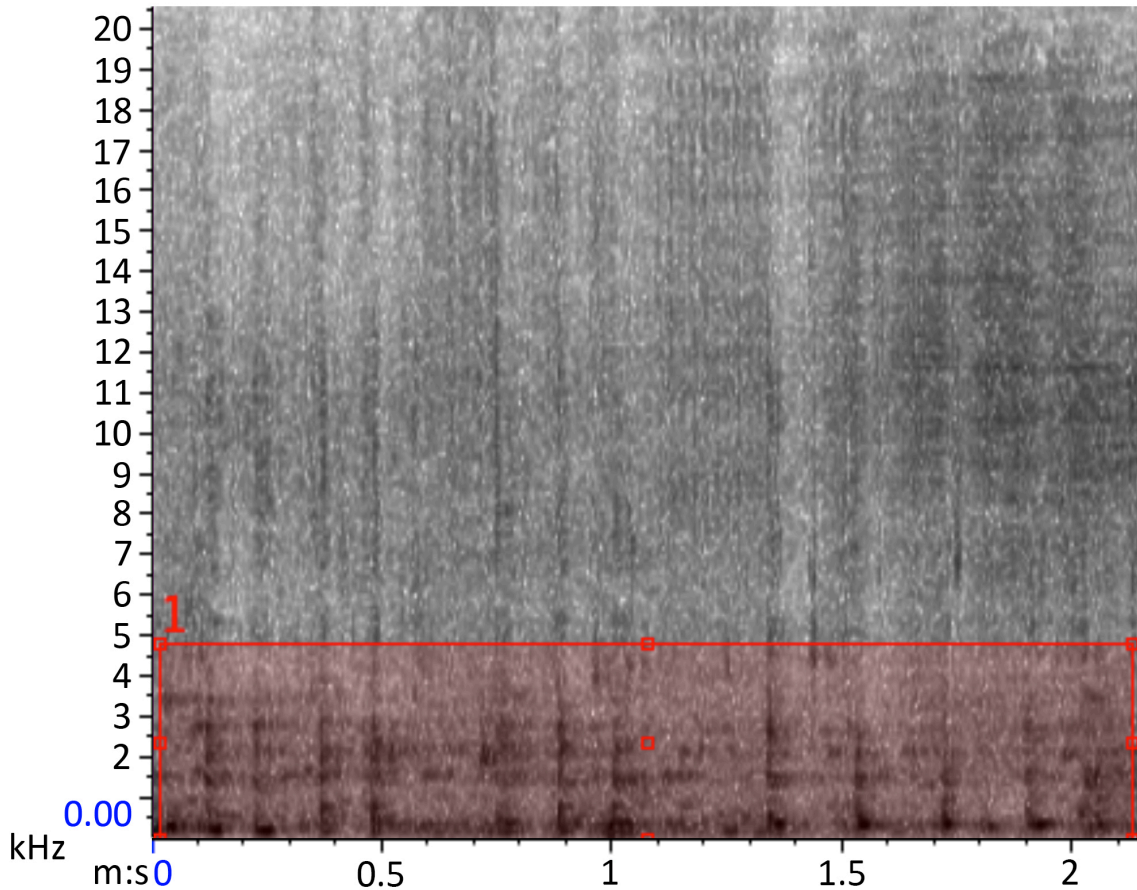


Figure 8. LHR thinks with peak frequencies near 0.5 kHz and harmonic structures extending towards 5 kHz. X-axis is in half-second intervals.

Without specifically defined parameters for “pops”, it is hard to know if HHR thinks were the sounds referred to by McCowan and Reiss (1995). Based on Vollmer et al.’s (2015) report, the pops discussed by McCowan and Reiss (1995) were likely not the same as pops described for the *aduncus* species. Therefore, it is possible that the pops mentioned by McCowan and Reiss (1995) are more similar to the HHR sound reported here. Regardless, evidence for sex-based differences between these two sounds could not be assessed, as the social group reported in the current study was all female. Thus, within an all-female group of bottlenose dolphins there was variation in the harmonic structures of these sounds. Based on this finding alone, the differences in *aduncus*-type pops and think sounds may be due to inter-population (or even interspecies) variation in communication repertoires.

Caveats and Conclusions

The principle limitation to this study was our inability to localize the mother as she produced sounds, as there was only one hydrophone available for use at the facility during the course of data collection. It was

possible that variability in harmonic structure was due to different dolphins producing their version of the thunk sound during events. We attempted to limit our data to periods when the mother and calf were the only animals near the hydrophone, however this does not rule out production of thunks by other females in adjacent pools during events as well.

BEL produced bubble streams coinciding with a number of thunks in the data set. While bubble streams may not accompany the majority of adult dolphin sounds, and as a result may not be representative of the adult's vocal repertoire (Fripp, 2005), the thunks produced on camera with bubble streams were strong evidence for BEL's use of these sounds. All thunks occurring simultaneously with bubble streams were produced in the first 20 days of the calf's life. It is possible that bubble streams are used as an additional display for a calf's identification of its calling mother. Once a calf associates sounds with its mother, bubble streams may no longer be necessary for the calf to distinguish the dolphin producing the thunk from remaining group members.

McCowan and Reiss (1995) and the current study are the only existing investigations into the thunk sound. Both studies were carried out with female bottlenose dolphins at the same captive facility. Furthermore, BEL is the daughter of CHE, one of the females in the original study. It is possible that the thunk sound is a learned signal specific to this group of dolphins, so it would be important to determine whether other *Tursiops truncatus* social groups employ this or similar sounds in the context of mother-calf separations. If such a sound exists within other dolphin social groups, this would be evidence for a biologically relevant sound in bottlenose dolphin mother-calf communication. Furthermore, if the thunk continues to be associated with separation events, as was identified here, then this sound may be one of the most contextually limited sounds produced by dolphins, and may encode information regarding threat or urgency of response. Given the findings reported here, we feel that thunks have far more diversity in acoustic structure than what has previously been documented. As such, this sound needs attention in future research as a contextually salient signal.

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