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Authors
Ames, Audra E
Macgregor, Riley P
Wielandt, Sara J
et al.

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Pre- and Post-Partum Whistle Production of a Bottlenose Dolphin
(*Tursiops truncatus*) Social Group

Audra E. Ames [1-2]**, Riley P. Macgregor** [1]**, Sara J. Wielandt** [3]**, Dianne M. Cameron** [3]**, Stan A. Kuczaj II** [1]**, and Heather M. Hill** [4]

[1] *The University of Southern Mississippi, U.S.A.*
[2] *Fundación Oceanogràfic de la Comunitat Valenciana, Spain*
[3] *Six Flags Discovery Kingdom, U.S.A.*
[4] *St. Mary's University, U.S.A.*

The signature whistle of the Atlantic bottlenose dolphin (*Tursiops truncatus*) is a well studied acoustic signal known for broadcasting identity and maintaining contact with conspecifics. Several studies have investigated the use of this signal surrounding the birth of calves to dolphin social groups, although some discrepancies exist between the findings of these studies. The current study was an attempt to reconcile some of the inconsistencies through the investigation of signature whistle production by a bottlenose dolphin group two months prior to and two months following the birth of a calf to one of the social group members. We found that the production of signature whistles matching the contour belonging to the dolphin mother increased significantly in both the pre- and post-partum period. Heightened production of the mother's signature whistle type in the first week of our focal calf's life supports the establishment of a recognition system within this time period. Given that learning processes associated with the sound environment appear to begin shortly after calf birth, we also explored the signature whistle rates of the other social group members in an effort to determine whether any signature whistle production influenced the development of the dolphin calf's own signature whistle type. We found that the signature whistles of the other social group members were produced significantly less than the mother's signature whistle until after the first week post-partum. Although the calf did not appear to develop a signature whistle during the length of the study, there was no substantial evidence that the whistles from other group members influenced the calf's whistle production.

Keywords: signature whistle, dolphin, calf, development, partum, maternal, production, rate

The signature whistle of the Atlantic bottlenose dolphin (*Tursiops truncatus*) is perhaps one of the most well studied acoustic signals in the cetacean literature. It has been widely established that these sounds are produced in contexts where maintenance of conspecific contact is necessary (e.g., during separations or locating of individuals, facilitating reunions, and maintaining group cohesion; Herman & Tavolga, 1980; Janik & Slater, 1998; Janik, Sayigh, & Wells, 2006; Sayigh, 1992; Sayigh et al., 1998; Smolker, Mann, & Smuts, 1993; Tyack, 1986), as individual identity is encoded in the contour shape of these signals (Janik et al., 2006). Signature whistle use within mother-calf dyads has also been well documented as these signals appear to have a critical function in mediating mother-calf recognition (e.g., Janik et al., 2006; Sayigh, Tyack, Wells, & Scott, 1990; Sayigh, Tyack, Wells, Scott, & Irvine, 1995; Sayigh et al.,

1998; Smolker et al., 1993).

Several studies have investigated the role of maternal signature whistle production surrounding parturition, as mother bottlenose dolphins have been shown to increase their signature whistle use prior to (Mello & Amundin, 2005) and following (Fripp & Tyack, 2008; King, Guarino, Donegan, Hecksher, & Jaakkola, 2016) the birth of a calf. Discrepancies exist between findings of these studies, however. For example, Mello and Amundin (2005) found that bottlenose dolphin mothers increased their signature whistle production during gestation, with the largest increase occurring in the days immediately preceding birth. It has been hypothesized that these pre-partum increases in maternal signature whistle production may aid in calf recognition of this sound shortly after birth by exposing the calf to the sound in utero (Kuczaj & Winship, 2015; Mann & Smuts, 1998; Mello & Amundin, 2005), but later studies have found no evidence substantiating this phenomenon in the pre-partum period (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016). Instead, these later studies reported heightened production of the mother's signature whistle in the weeks immediately following calf birth (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016). This increased post-partum production of the mother's signature may also be an underlying mechanism in the establishment of an early recognition system in the mother-calf dyad (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016), but there appears to be some variability in the sensitive window during which this process occurs.

Fripp and Tyack (2008) found that peak production of the maternal signature whistle occurred in the first week of calf life, with whistle rates returning to baseline (i.e., pre-partum production rates) by the third week post-partum. The authors speculated that this trend corresponded with an imprinting hypothesis posited by Mann and Smuts (1998), which predicted the increase of maternal signature whistles in the first week of life based on the behavior of dolphin (*Tursiops aduncus*) mothers in Shark Bay, Australia during this same time period. During the first week of life, mothers appear intolerant of social separations, whereby newborns depart from the dyad to join other dolphins. Once mothers become more tolerant of these social separations with calf age and increased independence, signature whistle production should decline (Fripp & Tyack, 2008; Mann & Smuts, 1998).

King, Guarino, Donegan and colleagues (2016) found that the dolphin mothers in their study maintained high whistle rates for a month post-partum and that whistle rates declined irrespective of increased calf independence, which occurred two weeks after maternal signature whistles dropped in production. It should be noted that the authors reported a calf switch between the two focal dyads occurring in the third post-partum week and, as such, whistle rates may have been skewed by the event (King, Guarino, Donegan et al., 2016). However, King, Guarino, Donegan and colleagues (2016) still suggested that the window for calf imprinting was longer and more flexible than previously believed. These two characteristics are contrary to the notion of imprinting in the classic sense (Lorenz, 1937), as this process should occur in a limited sensitive window following birth and have a degree of irreversibility. Furthermore, imprinting appears to be a more biologically based process that does not take into account calf attachment to allo-mothers. Given the findings presented by King,

Guarino, Donegan et al. (2016), it is more likely that learning influences the establishment of an early recognition system within a mother-calf dyad more so than imprinting, although the underlying mechanisms for both need not be mutually exclusive.

Non-maternal signature production appears reduced (Fripp & Tyack, 2008) or static (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016) with the addition of a new calf to a social group. This reduction in additional signature stimuli may aid a dolphin neonate in learning its mother's signature through decreased exposure of the calf to other sounds in the environment. However, sounds that are not produced commonly in the sound environment may also aid a dolphin calf in its own signature whistle acquisition (Fripp et al., 2005). Calves develop their signature whistles through vocal production learning, incorporating acoustic models available in their environment into their vocal repertoires (Caldwell & Caldwell, 1979; Fripp et al., 2005; Miksis, Tyack, & Buck, 2002; Sayigh, 1992; Tyack, 1997; Tyack & Sayigh, 1997). In wild populations, calves generally develop signature whistles that are dissimilar to their mother's own whistle, opting to model whistles based on those of unrelated or loosely associated conspecifics instead (Fripp et al., 2005; Sayigh, 1992; Tyack, 1997). In captive social groups, calves show similar behavior, modeling their signature whistles after other social group members (Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997) or marking stimuli (Miksis et al., 2002; Sayigh, 1992; Tyack, 1997). As calf behavior and development may be shaped by learning processes associated with the sound environment in early life, perhaps the rates of other signals during this period of time may influence the ontogeny of whistles in the calf's vocal repertoire.

Due to discrepancies in the current literature, it was our aim to provide more information regarding trends of the maternal signature whistle type surrounding parturition. We studied a mother-calf dyad in an effort to determine if signature whistle increases in the pre-partum period are truly unusual based on the rarity of this phenomenon in the literature. Moreover, we explored post-partum increases to further evaluate the time window of their occurrence and assess learning processes that may be associated with establishment of a recognition system between a mother and her calf. Finally, we provide an investigation into the signature whistle types of other social group members as they relate to maternal signature whistle production in the pre- and post-partum periods and calf whistle repertoire development.

Method

Study Animals, Facility, and Data Collection

Data were collected from the Marine Research Center (MRC) habitat at Six Flags Discovery Kingdom (Vallejo, CA). At the time of the study, the habitat housed six adult, female Atlantic bottlenose dolphins. The study's focal dyad included a 9-year-old primiparous mother (BEL) and her calf (MIR), born January 9, 2014. The five remaining adult social group members were CHE (age 34 at the time of study), JAS (age 26), MAT (age 8), YOS (age 10), and PIN (age 16). CHE was the mother of BEL and grandmother of MIR.

The data collection period for the current study was comprised of two months (56 days) prior to

and two months (56 days) following MIR's birth. Data for the pre-partum period were collected from November 14, 2013, to the calf's birth, at which point data collection for the post-partum period began and continued until March 5, 2014. MIR passed away about a month after the conclusion of the study. During the course of our study, however, health assessments indicated a healthy and developing calf. We also had access to incomplete data sets involving calf births from other females of the social group after the completion of this study, which we used in confirming the signature whistle contours of some group members (see *Adult whistle classification*). Data were collected sporadically for PIN (calf birth March 17, 2014 to calf death March 28, 2014), MAT (unknown date, calf birth and death on same day in January/February 2015), and YOS (calf birth February 5, 2015).

Data were recorded opportunistically throughout the day almost daily over the course of the study. Acoustic data were recorded with a CR-1 hydrophone (linear frequency range: 0.16 Hz - 48 kHz +/- 3 dB; Cetacean Research Technology, Seattle, WA), placed in an acoustically transparent, cylindrical tube adjacent to the viewing window of MRC's center pool (Figure 1), and a Sony Audio Recorder PCM-M10 (frequency response: 20 Hz - 40 kHz at 96 kHz sampling rate). However, acoustic 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 (placed in front of the center pool's observation window). Inputting sound through the Vixia HF200 allowed for under water recordings to sync with behaviors recorded by the camera. These synced behavioral and acoustic recordings were primarily collected for a concurrent study on the "thunk" vocalization produced by this social group (Ames et al., 2017) but were also used for associating bubble streams with MIR's whistles in the current study (method reviewed in *Calf whistle identification*) and to identify any potential confounding interactions that may have biased signature whistle rates (e.g., calf stealing by other dolphins, training sessions involving the dyad or other animals, physical introductions of calf to other dolphins). Data in which the video and hydrophone recordings were not synced were excluded from the study in order to eliminate any acoustic data in which dolphin behavior was unknown.

The center pool of the MRC habitat was an oval pool approximately 13 m wide, 18 m long, and 4.5 m in depth. The adjacent pools were cylindrical pools approximately 15 m in diameter and 4.5 m in depth. Each pool could be closed off from the others via an acoustically transparent gating system so that when the mother and calf were physically isolated in the center pool during the calf's early life, the acoustic signals could still be transmitted from other pools into the sound environment of the center pool and recorded by the CR-1 hydrophone. Because the study employed the use of a single hydrophone and sounds were still easily transmitted from other pools in the habitat, it was difficult to localize signaling individuals. Consequently, we focused our effort in determining the overall rates of the signature whistle types produced.
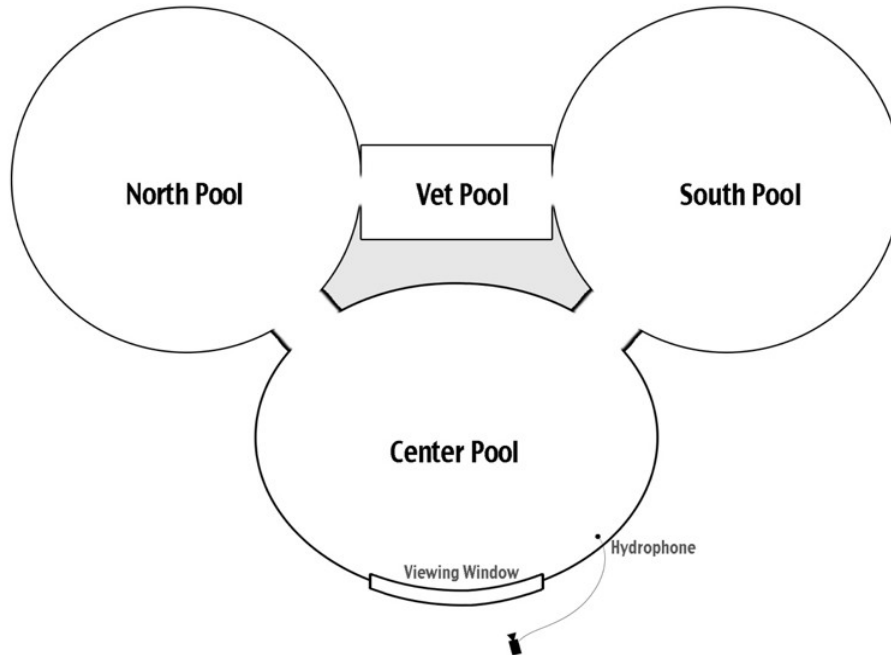
Figure 1. **MRC habitat at Six Flags Discovery Kingdom accompanied by placement of video camera and hydrophone recording device.**

During the pre-partum period, the gate between the north and center pools remained open, allowing BEL, JAS, CHE, and MAT to swim freely between the two pools. Access between these pools was closed beginning the day of MIR's birth, with the dyad becoming the center pool's primary occupants for the first few weeks of MIR's life. CHE and JAS were individually allowed in the pool with the dyad shortly after the calf's birth (first CHE and then JAS), as BEL was initially not responsive to MIR. Whistle rates for these interactions were not included in data analyses for the study due to an unexpected hydrophone malfunction from January 7-9. While unfortunate that we could not record on these dates, this lack of data also eliminated the inclusion of increases in signature production resulting from separating the dyad from other companions immediately after birth. BEL's response to her calf returned to normal (e.g., swimming with MIR in slip-stream, allowing nursing, disallowing separations from the dyad) on January 10, 2014. Subsequently, inclusion of data for the post-partum period began the day following MIR's birth, once the dyad had been gated alone in the center pool for some time.

Occasional physical introductions of the dyad to other group members began occurring at the end of the first week of MIR's life. CHE was gated in the center pool with the dyad on January 15 and moved back to the north pool on January 16. MAT was housed with the dyad on January 24, February 7, and February 15. Data from these dates were not excluded from analyses of whistle rates as there were no increases of any contour type following the introduction or separation of either CHE or MAT to the dyad. On February 18, the gate to the north pool was opened for the remainder of the study, allowing BEL, MIR, CHE, and MAT to swim freely between the north and center pool. JAS was added back to the social group in the center and north pools on February 19 after a temporary move to the south pool on the February 18. YOS and PIN remained in MRC's south pool, physically separated from the dyad for the entirety of the study.

Data

For analyses, data were divided into 16 one-week periods (eight periods pre-partum and eight periods post-partum) so that increases within a week could be compared to previous studies using similar sampling periods (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016). Approximately 80 hr of data were analyzed for the entire study (approx. 5 hr sampled from each week, opportunistically from the days during which recordings were acquired).

Data were analyzed in Raven Pro 1.4 and 1.5 (Cornell University) using a Hann window (512 window size) with DFT of 512, 50% overlap and 256 sample hop size. For adult whistle classification and calf whistle identification, one rater (AEA) reviewed all 80 hr of sampled data, as human judges are superior in contour matching when compared to quantitative methods (Janik, 1999; Sayigh, Esch, Wells, & Janik, 2007). AEA classified each adult whistle based on an all-occurrence sampling method (King, Guarino, Donegan et al., 2016). AEA's classifications were then subjected to review by two raters unfamiliar to whistles produced by the MRC dolphins (see *Statistical Analyses* for inter-rater reliability measures).

Adult whistle classification. In August 2014, one author (AEA) collected the signature whistles of all adult dolphins in the study's social group (excluding PIN, discussed further below) to create the signature whistle classification catalog used in contour matching. Each female had previously been trained to produce her signature whistle (based on whistles she produced in isolation and/or the main whistle type mothers used with their calves) when presented with an associated discriminatory hand signal (S^D). For signature whistle collection, all dolphins were asked to station pool-side simultaneously so that their melons (i.e., the structure through which odontocetes are believed to direct sound; Cranford, 2000; Cranford, Amundin, & Norris, 1996; Madsen, Lammers, Wisniewska, & Beedholm, 2013; Madsen, Wisniewska, & Beedholm, 2010) were out of the water to limit the possibility that recorded underwater whistles belonged to another animal. Each dolphin was then sent individually from the trainer pool-side to a second trainer (author SJW). Once the individual dolphin was positioned with SJW, the dolphin was asked to produce her signature whistle using the previously trained S^D. This procedure was repeated three to six times for each animal over a two-day period, so that multiple instances of each animal's signature could be included in the classification catalog.

We also used two additional peer-reviewed methods to confirm this initial signature typing. First, we employed the sequential SIGID method (Janik, King, Sayigh, & Wells, 2013) in order to confirm that each signature whistle type could be classified as such. Based on this method, each type was classified as a signature if at least 75% of matching contours within a bout (i.e., a continued repetition of a signal) occurred within an interval of 1-10 s from a previous or subsequent iteration (Janik et al., 2013), with loops occurring less than 250 ms from the initial loop (Esch, Sayigh, Blum, & Wells, 2009; Janik et al., 2013). We analyzed opportunistic recordings of each contour type per week period that contained a minimum of four whistles (Janik et al., 2013) within a minute time frame in order to reduce potential for error in signature whistle assumption by comparing data across sessions and recordings for the same individuals (Janik et al., 2013). Secondly, we reviewed data in which animals were isolated from other group members (JAS, CHE, MAT, BEL, YOS) or in days following the birth of a calf, during which animals were alone with their calves (BEL, YOS, MAT) in order to confirm allocation of each whistle type to the correct animal. We selected these contexts, as signature whistle production by the focal animals were highly likely due to social group isolation (Caldwell & Caldwell, 1965) and calf-directed signature whistle production (Kuczaj, Eskelinen, Jones, & Borger-Turner, 2015; King, Guarino, Keaton, Erb, & Jaakkola, 2016).

In addition to the five whistle types collected on S^D for BEL, CHE, MAT, JAS, and YOS, two other prominent whistle contours meeting the above SIGID classification criteria appeared consistently in the dataset and were included in analyses as a result. One additional signature contour was determined to belong to MAT through its production in several recordings obtained after the completion of the current study during which MAT was isolated from the social group. We termed this whistle MAT1 and the contour collected on S^D for MAT, also produced when MAT was isolated in the same recordings, as MAT2. MAT was the only animal for which a secondary signature (Kuczaj et al., 2015) was apparent in the dataset. Whistle B was the second additional prominent contour type, which appeared to be a shared whistle type of this particular social group based on findings from previous studies conducted at the same facility (whistle type 2; McCowan & Reiss, 1995a, 1995b, 1997, 2001). PIN's signature whistle was never identified as, at the time of the study, she was the only MRC female not trained on S^D to produce her signature whistle, and no other prominent whistle types could be identified as belonging to her through our additional

methods. We reviewed data during which PIN was socially isolated and immediately following the birth and death of PIN's calf and found no uncatalogued whistle contours meeting SIGID classification criteria. Finally, all variant whistle types or whistles that could not be classified as a signature contour were classified as "other". In the post-partum period, the "other" classification also included potential calf whistles that could not be positively identified as belonging to MIR. Figure 2 summarizes the contour types used for classification.
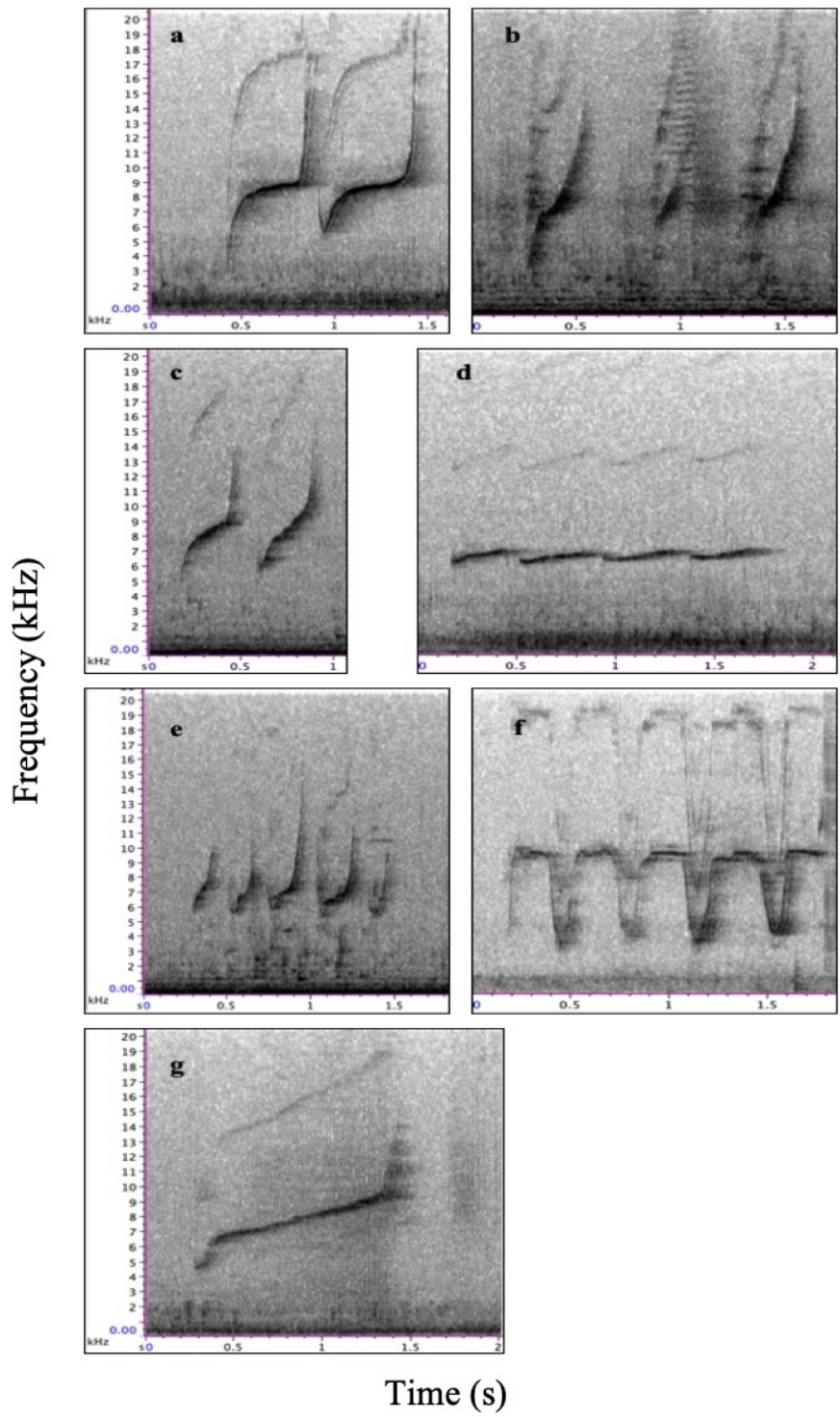
Figure 2. **Contour of each major whistle type: (a) BEL, (b) JAS, (c) CHE, (d) MAT1, (e) MAT2, (f) YOS, (g) Whistle B.**

Calf whistle identification. Bubble stream methodology was employed for identifying whistles that belonged to MIR. Calf whistles are generally distinguishable from adult whistles in early life as they are tremulous and squawky in nature (Killebrew, Mercado, Herman, & Pack, 2001). Any whistles with these features within the data set were subsequently reviewed in the video data to determine if a simultaneous bubble stream emitted by MIR could be paired with the whistle emission. If MIR was on screen in the synced video recordings producing a clearly visible, coinciding bubble stream with a calf-like whistle in the acoustic recordings, this whistle was attributed to MIR. It is important to note that the bubble stream method may not allow for full representation of a calf's vocal repertoire as it is a highly conservative method in localizing the vocalizations of adult dolphins (Fripp, 2005). However, bottlenose dolphin calves purportedly produce vocalizations with associated bubble streams in much of early life (McBride & Kritzler, 1951; McCowan & Reiss, 1995b), as odontocete calves in general may lack the muscular development or motor control necessary to seal the blowhole, preventing air leakage from the vestibular air sacs during vocal production. Furthermore, while the bubble stream method has been realized as a conservative technique for localizing adult dolphin vocalizations, many ontogenetic studies have employed this methodology when identifying odontocete calf sounds (Bojanowski, Veit, & Todt, 2000; Bowles, Young, & Asper, 1988; Favaro, Gnone, & Pessani, 2013; Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Hooper, Reiss, Carter, & McCowan, 2006; Killebrew et al., 2001; McBride & Kritzler, 1951; McCowan & Reiss, 1995b; Mello & Amundin, 2005; Miksis et al., 2002; Morisaka, Shinohara, & Taki, 2005a, 2005b; Reiss, 1988; Vergara & Barrett-Lennard, 2008).

Parameter extraction. In order to investigate potential whistle types included in MIR's developing vocal repertoire, we compared parameters extracted from MIR's whistles to parameters extracted from the adult whistle types. Using the previously identified spectrogram parameters in Raven, we extracted the beginning, end, maximum, and minimum frequencies as well as the frequency range, duration, and number of inflection points for whistles that met inclusion criteria for parameter extraction (see Table 1 for parameter operational definitions). In order for whistles to meet inclusion criteria for parameter extraction, whistles were required to have a high signal to noise ratio and could not be overlapped by other whistles or noise.

Table 1

Definitions of Whistle Parameters

Parameter	Definition
Beginning Frequency (kHz)	Frequency at which whistle begins
End Frequency (kHz)	Frequency at which whistle ends
Maximum Frequency (kHz)	The highest frequency of the whistle
Minimum Frequency (kHz)	The lowest frequency of the whistle
Frequency Range (kHz)	The difference between the minimum and maximum frequency
Duration (s)	The length of the whistle in seconds from the beginning to end frequency
Inflection Points	A point in the whistle at which the contour changes direction (e.g., ascending to descending)

Statistical Analyses

Inter-rater reliability. To reduce potential biases in whistle categorization, 10% of the data set ($n = 8$ hr) was used to measure inter-rater reliability. Data were randomly selected from each week and then subjected to contour matching by two raters that were naïve to the whistles of the MRC dolphins. The raters were given the main whistle contours and then asked to complete the contour matching task using the given data. Raters were also asked to identify any potential calf whistles within the data set as well.

Rates of each contour matched by the raters were then compared and required to have a correlation coefficient (Pearson's r) of 0.8 or higher. Raters were in high agreement on primary whistle type categorization ($r = 0.98$), "other" whistle types pre-partum
($r = 0.92$), "other" whistle types post-partum ($r = 0.90$), and identification of potential calf whistles ($r = 0.84$).

Adult whistle rates. As previously mentioned, an all-occurrence sampling method was used so that all adult whistles were included in whistle type analyses. Continuous and noncontinuous multi-looped whistles were counted as a single whistle emission (Caldwell, Caldwell, & Tyack, 1990; Tyack, 1997). As we were unable to localize individual whistle types to vocalizing animals, rates encompassed all contours matched to a specific signature whistle contour, including whistles produced by the individual to which the signature was ascribed and any potential copies produced by other social group members (King & Janik, 2013; King, Sayigh, Wells, Fellner, & Janik, 2013). Thus, rates were calculated by dividing the number of dolphins in the habitat per minute of data analyzed for each week for dolphin-per-minute whistles rates (Fripp & Tyack, 2008). Consistent with previous studies (Fripp & Tyack, 2008; Mello & Amundin, 2005), we used one-way ANOVAs to determine the highest rates of each whistle type over time in addition to comparing the totals of each whistle type. Brown-Forsythe tests were used in place of ANOVAs when homogeneity of variance assumptions were violated and all groups had variance (i.e., some periods were characterized by zero emission of a type). Games-Howell post hoc tests were used in all pairwise comparisons when unequal variances were assumed. "Other" whistle rates were used in comparison of all whistle types overall but were not included in statistical analyses of the primary whistle contour types within time periods.

Calf whistle development. Parameters extracted from all calf whistles in each of the eight weeks post-partum (weeks 9-16) were compared to parameters extracted from each of the main adult whistle contours using a discriminant function analysis (DFA). We excluded Whistle B and "other" whistles in the DFA, only using whistles we believed to be contours belonging to individuals in the analysis. Contrary to whistle rate analyses, each loop of multi-looped whistles was treated as an individual whistle for the DFA so that variability within whistle signature types was included in the model. Parameters extracted from loops were then randomly sampled from both the pre- and post-partum periods for inclusion in the DFA based on the lowest number of loops emitted for one of the adult female's whistle type (JAS: $n = 215$). Inflection points were excluded from the DFA as these were a discrete variable; however, inflection points as a measure of whistle stability in the calf's developing repertoire are briefly discussed below.

Results

Adult Whistle Rates

A total of 14,273 whistles were included in the overall analyses for adult whistle rates. Whistles matching BEL's contour and MAT1 were produced significantly more (Games-Howell: $p < 0.001$) than the contour types matching other group members' whistles (Figure 3), Brown-Forsythe: $F(7, 549.54) = 302.59$, $p < 0.001$, but were not significantly different from each other (Games-Howell: $p = 0.93$). Whistle contours matching CHE, MAT2, and Whistle B were produced moderately over the course of the study and were also not significantly different from each other (Games-Howell: $p > 0.05$). Rates of whistles matching JAS and YOS signature contours were not

significantly different (Games-Howell: $p = 0.08$) and were produced significantly less than all other whistle types (Games-Howell: $p < 0.05$). Table 2 details the total whistles and descriptive statistics for each whistle classification.

Production of whistles matching BEL's contour, ANOVA: $F(15, 349) = 65.68$, $p < 0.001$, significantly peaked in the pre-partum period during week six ($M = 0.44$, $SD = 0.16$, Games-Howell: $p < 0.001$). This period marked the highest rate of production overall during the course of the study. The second highest increase in BEL's signature whistle type occurred in the first week post-partum (week nine: $M = 0.18$, $SD = 0.15$). After the first week post-partum, rates of BEL's whistle type significantly dropped (Games-Howell: $p < 0.05$).
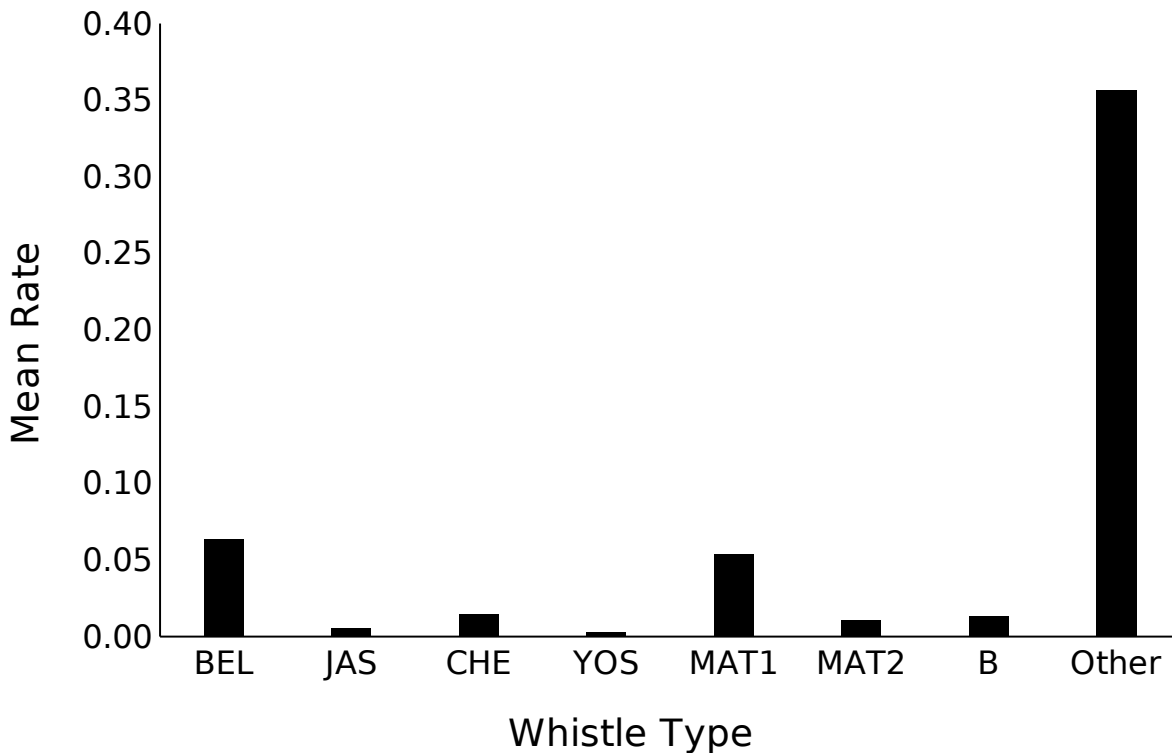

Figure 3. **Mean (*M*) of total whistle rate for each whistle type.** Means were calculated by dolphin-per-minute. Error bars equal the standard deviation values (*SD)*.

Table 2

Total Number of Whistles, Percentage of Total Whistle Production, and Descriptive Statistics for Each Whistle Type

Dolphin	Total	% of Total	M^a	SD

BEL	1837	12.87	0.06	0.12
JAS	181	1.27	0.01	0.01
CHE	432	3.03	0.01	0.03
YOS	100	0.70	0.003	0.01
MAT1	1841	12.90	0.05	0.10
MAT2	304	2.13	0.01	0.02
B	408	2.86	0.01	0.03
Other	9170	64.25	0.36	0.33
Total	14273		0.07	0.17

Note. ªMeans (*M*) were calculated by dolphin-per-minute.

Rates of contours matching BEL's signature whistle, Brown-Forsythe: $F(6, 202.57) = 40.14$, $p < 0.001$, were significantly higher (Games-Howell: $p < 0.001$) in the pre-partum period than the contour types of other group members. The same was true for the first week post-partum, ANOVA: $F(6, 154) = 23.70$, $p < 0.001$, as whistles matching BEL's signature contour were produced significantly more than all other main contour types (Games-Howell: $p < 0.05$). Whistles matching the non-maternal contours began to increase following the first week post-partum (Figure 4). Comparison of contour type production in weeks 10-16 (weeks 2-8 post-partum), Brown-Forsythe: $F(6, 289.93) = 70.85$, $p < 0.001$, showed that whistles matching BEL's signature contour were not significantly different from CHE (Games-Howell: $p = 0.95$) or MAT2 (Games-Howell: $p = 0.20$). Production of whistles matching the MAT1 contour was significantly higher than all other contour types in weeks 10-16 (Games-Howell: $p < 0.001$).
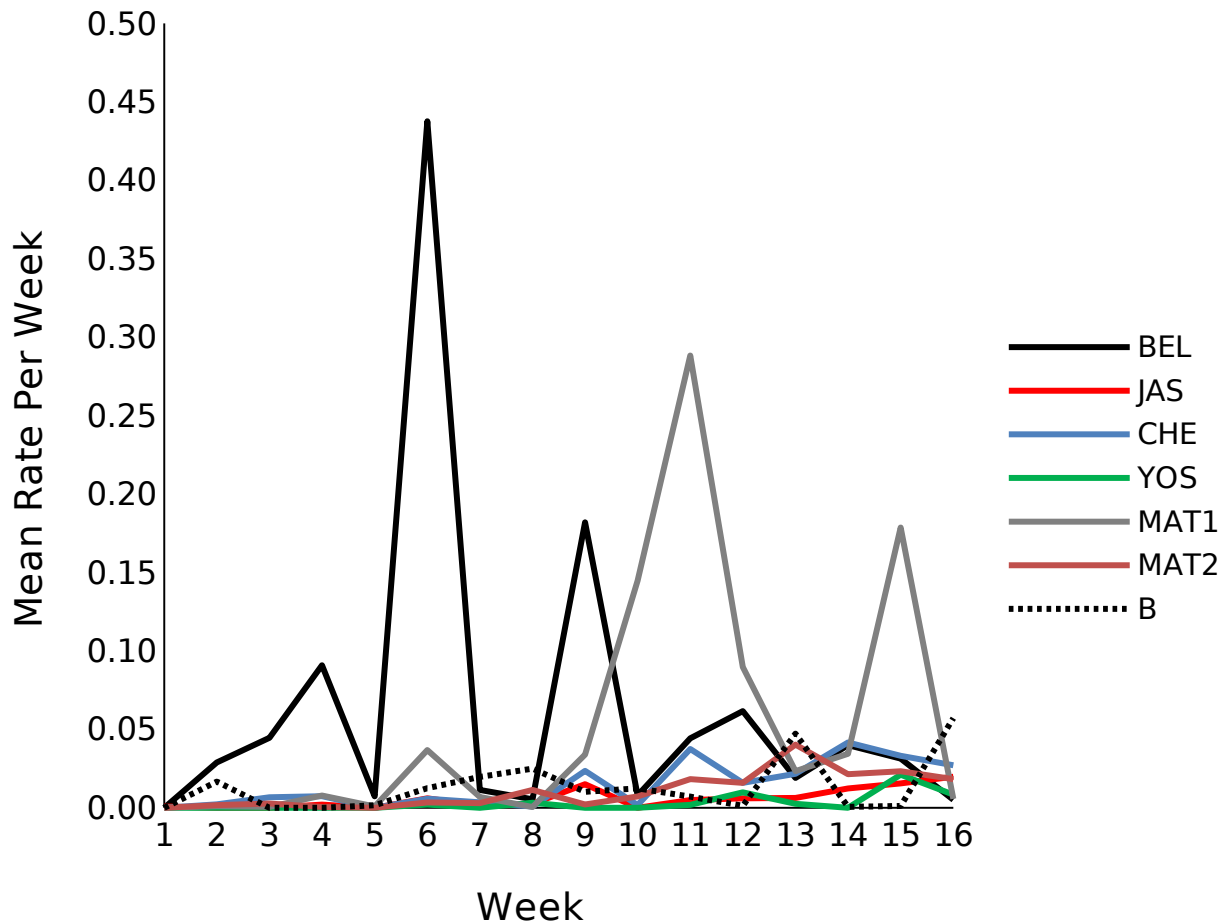
Figure 4. **Mean of each whistle type per week.** Means were calculated by dolphin-per-minute.

Calf Whistle Development

A total of 350 calf whistles were used for parameter extraction and subsequent comparison to the whistles believed to be signatures of the adult social group members. Fourteen possible groups were included in the DFA: six groups corresponding with each adult contour type and eight groups corresponding with parameters extracted from calf whistles from each post-partum week. Overall, calf whistles were primarily classified as belonging to calf whistle groups (Table 3), especially in the earlier weeks of life. MAT1 and MAT2 were the adult groups for which predicted group membership of MIR's whistles was most consistent. The same was true when calf whistles were treated as a single group, as a second DFA indicated that

calf whistles belonged to the calf group in 58.3% of cases. Of the adult groups, calf whistles were grouped with MAT2 in 14.3% of cases and with MAT1 in 10.9% of cases (Figure 5). It did not appear that MIR began to develop a signature whistle of her own during the course of the study, as no one whistle type was prominently produced overall. However, it did seem that calf whistles progressed and became more adult-like as evident by the decrease in the range of inflection points over time. In MIR's first month of life, the maximum range of inflection points (range: 4 - 8) was much higher than the maximum range of inflection points in the second month (range: 2 - 4).

Table 3

Predicted Group Membership for the Calf Whistles of Each Post-Partum Week

	Whistle Classification														
	Adult Whistle Groups						Calf Whistle Groups by Week								
Week	BEL	JAS	CHE	YOS	MAT1	MAT2	9	10	11	12	13	14	15	16	Total
9	10	0	0	6	6	1	30	10	4	7	5	0	5	4	88
10	1	1	0	3	3	1	16	16	1	7	3	0	0	2	54
11	0	3	0	4	2	3	11	4	3	11	3	0	6	6	56
12	1	2	0	0	2	1	3	0	1	7	2	1	2	0	22
13	1	0	0	2	1	3	11	5	0	9	17	0	2	3	54
14	0	0	0	0	1	0	3	0	0	1	1	1	1	1	9
15	0	0	1	1	5	13	4	0	0	1	2	1	9	5	42
16	1	2	2	0	0	8	2	1	0	3	1	0	5	0	25
Total	14	8	3	16	20	30	80	36	9	46	34	3	30	21	350
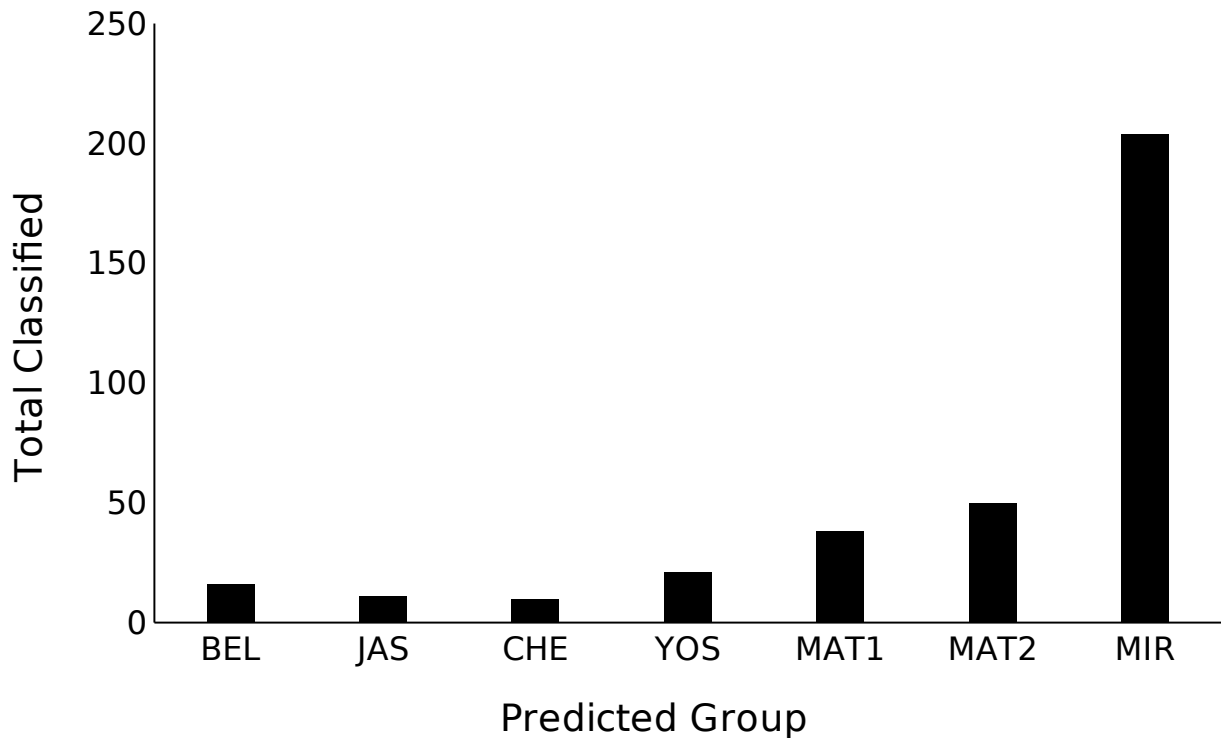
Figure 5. **Total number of calf whistles classified according to the predicted group membership of the discriminant function analyses with calf whistles as a single group**.

Discussion

Adult Whistle Trends

Whistles matching BEL's signature contour increased significantly in both the pre- and post-partum periods. The highest peak in production of this contour occurred in the sixth week of the study, three weeks prior to the end of the gestation cycle. This finding was surprising as it contradicts the findings reported by all previous studies of signature whistle production in the pre- (Mello & Amundin, 2005) and post-partum (Fripp & Tyack, 2008; King, Guarino, Donegan et al., 2016) periods. We reviewed the behavioral data recorded during week six, but, save for a 15-min period on one day during which BEL appeared on camera alone in the center and north pools, nothing else appeared as an obvious influence on the whistle rates of this time period (e.g., other dolphins were with her in the pools the remainder of the time, no training sessions occurred during recording). Furthermore, increases in BEL's signature whistle type during week six were not matched in response by increased production of signature contours by the remaining group members.

Overall, BEL's signature contour was produced significantly more in the pre-partum period than the other primary contour types. If BEL was the primary producer

of her own signature during the gestation period, one interpretation would suggest that some calf-directed learning processes may begin with the calf still in utero (Kuczaj & Winship, 2015; Mann & Smuts, 1998; Mello & Amundin, 2005). Prenatal sound exposure has been suggested to aid dolphin calves in whistle development (Tyack & Sayigh, 1997), and exposure to sound in utero appears to aid learning processes in humans (e.g., DeCasper & Fifer, 1980; Partanen, Kujala, Tervaniemi, & Huotilainen, 2013) and other nonhuman mammals (guinea pigs, *Cavia porcellus*, Vince, 1979; sheep, *Ovis aries*, Vince, Armitage, Walser, & Reader, 1982). If dolphin calves process sound in utero, exposure to the mother's signature whistle prior to birth may decrease the calf's fear response to the sound following birth, inciting the calf to follow the object with which it is already familiar (Van Kampen, 1996). Alternatively, dolphins may increase signature production when stressed (Esch et al., 2009), and mothers may be stressed or restless prior to labor (Mello & Amundin, 2005) as cortisol increases during gestation, peaking near delivery (Tizzi, Accorsi, & Azzali, 2010). However, this stress-related hypothesis does not explain the post-partum increase in BEL's contour type during week nine (first week of MIR's life), once the stress of labor would have subsided, or why the production of BEL's signature slowed in the two weeks prior to MIR's birth, as stress would have presumably increased during this time.

During the post-partum period, production of whistles matching BEL's signature type were significantly higher in the first week of MIR's life. This pattern corresponds to findings from Fripp and Tyack (2008) and provides additional empirical support for the establishment of a recognition system in the first week following birth. Furthermore, its logical that this process would occur as soon after birth as possible, as dolphin neonates are precocial and have the propensity to engage in behavior detrimental to survival by following accelerated objects immediately after birth (Connor, Wells, Mann, & Read, 2000; Mann & Smuts, 1998). Calves may swim after adult social group members that may not be invested in the calf's life, so it would be advantageous for recognition to be established within a dyad immediately following birth in order to increase the chances of calf survival. Therefore, we believe that calf recognition of the mother's signature is established closer to birth and in a less variable time frame than what was hypothesized by King, Guarino, Donegan and colleagues (2016). However, it is likely that recognition is learned and can thereby be modified to fit mother-like figures in cases of allo-parenting, calf rejection, or calf switching.

The low production of non-maternal signature types during the pre- and post-partum periods may also enhance calf familiarity with the mother's sound. Most of the non-maternal primary contour types increased following the first week post-partum while production of BEL's signature significantly lowered. This pattern was especially true for the MAT1 contour, which was produced significantly more during weeks 10-16 than the other main contours classified for this study. MAT was housed initially with BEL and MIR more so than other group members during this period and was the youngest dolphin and least experienced with a calf. It was possible that these circumstances resulted in an elevated MAT1 response during weeks 10-16, but it was difficult to adequately investigate this hypothesis given the time constraints of this study.

Calf Whistle Repertoire

We were also interested in determining whether rates of any of the signature whistle types had an impact on the prevalence of whistles included in the calf's vocal repertoire. Based on the DFA's predicted group membership, MIR did not appear to commonly produce a whistle matching the parameters of her mother's contour type, which is not surprising given that bottlenose dolphin calves often develop signature whistles that are dissimilar to their mother's signature (Bojanowski et al., 2000; Caldwell & Caldwell, 1979; Fripp et al., 2005; Miksis et al., 2002; Sayigh, 1992; Tyack, 1997; Tyack & Sayigh, 1997). The outcome of MIR's whistle development beyond the first eight weeks of life remains unknown as the study was discontinued. However, at the study's termination, MIR had yet to produce an obvious signature whistle of her own.

Most commonly, MIR's whistles were classified as one of the eight calf whistle groups; likely a result of neonate inability to produce more adult-like sounds (Killebrew et al., 2001). The calf did appear to produce whistles matching each of the primary adult contours throughout the course of the study though, with calf whistles matching MAT1 and MAT2 types most frequent in comparison to the calf whistles matching the other adult contours. This trend is curious given that MAT spent the most time with the dyad, as compared to other social group members, prior to the dyad's integration back into the social group during MIR's second month of life. Moreover, both MAT contours were not rare during the course of the study, so if MIR had developed a signature matching either of MAT's contours later in life, this behavior would have varied from wild calves that model their signature whistles from dolphins that may have few social interactions with a dyad (Fripp et al., 2005). This finding still aligns with studies of dolphin calves in managed care that model their signatures based on conspecific whistles common in the environment (Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997).

Conclusions

It was the aim of this study to address some of the discrepancies in the current literature regarding maternal signature whistle production and calf birth. Although based only on one mother-calf dyad, the current study supports the establishment of an early recognition system within a dolphin mother-calf dyad sometime in the first week of life, especially when considered within the context of the previous literature. There is some potential that exposure to the maternal signature begins in utero as our study also provides additional evidence for increases in the maternal signature whistle type in the pre-partum period, but this is mostly speculation as there is still a large amount of variability in pre-partum maternal signature production between studies.

The rates of the other social group members' contour production may have influenced the repertoire of our focal calf, but more research exploring the relationship between non-maternal signature whistle rates and calf repertoire development may

allow for additional insight regarding learning processes associated with vocal development in early life. As we previously stated, if calf behavior is shaped by learning processes associated with the sound environment in early life, signals other than the mother's signature emitted during this period of time may be influential to calf development as well. The extent of this relationship deserves further exploration.

Acknowledgments

References

Ames, A. E., Zapetis, M. E., Witlicki, K. L., Wielandt, S. J., Cameron, D. M., Walker, R. T., & Kuczaj, S. A. (2017). Thunks: Evidence for varied harmonic structure in an Atlantic bottlenose dolphin (*Tursiops truncatus*) sound. *International Journal of Comparative Psychology*, *30*.

Bojanowski, E., Veit, F., & Todt, D. (2000). The development of a bivocal signature whistle in a bottlenose dolphin calf. *European Research on Cetaceans*, *14*, 70 –74.

Bowles, A. E., Young, W. G., & Asper, E. D. (1988). Ontogeny of stereotyped calling of a killer whale calf, *Orcinus orca*, during her first year. *Rit Fiskideildar, 11*, 251–275.

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). *Nature*, *207*, 434 –435.

Caldwell, M. C., & Caldwell, D. K. (1979) The whistle of the Atlantic bottlenosed dolphin *(Tursiops truncatus)* - ontogeny. In H. E. Winn & B. L. Olla (Eds.), *Behavior of Marine Animals* (Vol. 3, pp. 369-401). New York, NY: Plenum Press.

Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 199–234). San Diego, CA: Academic Press.

Connor, R., Wells, R., Mann, J., & Read, A. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Conner, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies* (pp. 91–125). Chicago, IL: The University of Chicago Press.

Cranford, T. W. (2000). In search of impulse sound sources in odontocetes. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing by whales and dolphins* (pp. 109–155). New York, NY: Springer.

Cranford, T. W., Amundin, M., & Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. *Journal of Morphology*, *228*, 223–285.

DeCasper, A., & Fifer, W. (1980). Of human bonding: infants prefer their mother's voices. *Science, 208,* 1174-1176.

Esch, H. C., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, *90*, 638–650.

Favaro, L., Gnone, G., & Pessani, D. (2013). Postnatal development of echolocation abilities in a bottlenose dolphin (*Tursiops truncatus*): Temporal organization. *Zoo Biology*, *32*, 210–215.

Fripp, D. (2005). Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, *21*, 29–44.

Fripp, D., & Tyack, P. (2008). Postpartum whistle production in bottlenose dolphins. *Marine Mammal Science, 24*, 479–502.

Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., Wells, R., & Tyack, P. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition, 8*, 17–26.

Gnone, G., & Moriconi, T. (2010). Use and function of distinctive whistle-like signals in bottlenose dolphins (*Tursiops truncatus*) mother-calf pair. In A. G. Pearce & L. M. Correa (Eds.), *Dolphins: Anatomy, behavior and threats* (pp. 149–167). Hauppauge, NY: Nova Science Publishers.

Herman, L., & Tavolga, W. (1980). The communication systems of cetaceans. In L. Herman (Ed.), *Cetacean behavior: mechanisms and functions* (pp.149–209). New York, NY: Wiley.

Hooper, S., Reiss, D., Carter, M., & McCowan, B. (2006). Importance of contextual saliency on vocal imitation by bottlenose dolphins. *International Journal of Comparative Psychology*, *19*.

Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behaviour*, *57*, 133–143.

Janik, V. M., King, S. L., Sayigh, L. S., & Wells, R. S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science, 29*, 109–122.

Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 8293–8297.

Janik, V. M., & Slater P. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour, 56*, 829–838.

Killebrew, D., Mercado, E., Herman, L., & Pack, A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, *27*, 34–44.

King, S. L., Guarino, E., Donegan, K., Hecksher, J., & Jaakkola, K. (2016). Further insights into postpartum signature whistle use in bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *32*, 1458–1469.

King, S. L., Guarino, E., Keaton, L., Erb, L., & Jaakkola, K. (2016). Maternal signature whistle use aids mother-calf reunions in a bottlenose dolphin, *Tursiops truncatus*. *Behavioural Processes, 126*, 64–70.

King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences, 110*, 13216–13221.

King, S., Sayigh, L., Wells, R. S., Fellner, W., & Janik, V. M. (2013). Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proceedings of the Royal Society*, *208*.

Kuczaj, S. A. II, Eskelinen, H. C., Jones, B. L., & Borger-Turner, J. L. (2015). Gotta go, mom's calling: Dolphin (*Tursiops truncatus*) mothers use individually distinctive acoustic signals to call their calves. *Animal Behavior and Cognition, 2*, 88–95.

Kuczaj II, S. A., & Winship, K. A. (2015). How do dolphin calves make sense of their world? In D.L. Herzing & C. M. Johnson (Eds.), *Dolphin communication and cognition: Past, present, and future* (pp. 201-226). Cambridge, MA: MIT Press.

Lorenz, K. (1937). The companion in the bird's world. *The Auk, 54*, 245–273.

Madsen, P. T., Lammers, M., Wisniewska, D., & Beedholm, K. (2013). Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: Clicking on the right side and whistling on the left side. *Journal of Experimental Biology, 216*, 4091–4102.

Madsen, P. T., Wisniewska, D., & Beedholm, K. (2010). Single source sound production and dynamic beam formation in echolocating harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology, 213*, 3105–3110.

Mann, J., & Smuts, B. B. (1998). Natal attraction: Kidnapping, allocare, and separations among wild bottlenose dolphin (*Tursiops truncatus*) mothers and infants. *Animal Behaviour, 55*, 1097–1113.

McBride, A., & Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy, 32*, 251–266.

McCowan, B., & Reiss, D. (1995a). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins, (Delphinidae, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. *Ethology, 100*, 193–209.

McCowan, B., & Reiss, D. (1995b). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, *109*, 242–260.

McCowan, B., & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: A comparison with humans and nonhuman animals. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 178–207). Cambridge, UK: Cambridge University Press.

McCowan, B., & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: A comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour*, *62*, 1151–1162.

Mello, I., & Amundin. M. (2005). Whistle production pre- and post-partum in bottlenose dolphins (*Tursiops truncatus*) in human care. *Aquatic Mammals, 31*, 169–175.

Miksis, J., Tyack, P., & Buck J. (2002). Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *The Journal of the Acoustical Society of America, 112*, 728–739.

Morisaka, T., Shinohara, M., & Taki, M. (2005a). Underwater sounds produced by neonatal bottlenose dolphins (*Tursiops truncatus*): I. Acoustic characteristics. *Aquatic Mammals*, *31*, 248.

Morisaka, T., Shinohara, M., & Taki, M. (2005b). Underwater sounds produced by neonatal bottlenose dolphins (*Tursiops truncatus*): II. Potential function. *Aquatic Mammals*, *31*, 258.

Partanen E., Kujala A., Tervaniemi M., & Huotilainen M. (2013). Prenatal music exposure induces long-term neural effects. *PLoS ONE, 8*, e78946.

Reiss, D. (1988). Observations on the development of echolocation in young bottlenose dolphins. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar* (pp. 121–127). New York, NY: Plenum Publishing.

Sayigh, L. S. (1992). *Development and functions of signature whistles of free-ranging bottlenose dolphins, Tursiops truncatus* (Unpublished doctoral dissertation). Massachusetts Institute of Technology, Cambridge.

Sayigh, L. S., Esch, H. C., Wells, R. S., & Janik, V. M. (2007). Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, *74*, 1631–1642.

Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins
Tursiops truncatus: Stability and mother offspring comparisons. *Behavioral Ecology and Sociobiology*, *26*, 247–260.

Sayigh, L., Tyack, P., Wells, R., Scott, M., & Irvine, A. (1995). Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, *36*, 171–177.

Sayigh, L., Tyack, P., Wells, R., Solow, A., Scott, M., & Irvine, A. (1998). Individual recognition in wild bottlenose dolphins: A field test using playback experiments. *Animal Behaviour, 57*, 41–50. doi:10.1006/anbe.1998.0961

Smolker, R. A., Mann, J., & Smuts, B. B. (1993). Use of signature whistles during separations and   reunions by wild
bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology*, *33*.

Tizzi, R., Accorsi, P. A., & Azzali, M. (2010). Non-invasive multidisciplinary approach to the study of reproduction and calf development in bottlenose dolphin (*Tursiops truncatus*): The Rimini Delfinario experience. *International Journal of Comparative Psychology*, *23*.

Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of   signature whistles?
Behavioral Ecology and Sociobiology, 18, 257.

Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics*, *8*, 21–46.

Tyack, P. L., & Sayigh, L. S. (1997). Vocal learning in cetaceans. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 208–233). Cambridge, MA: Cambridge University Press.

Van Kampen, H. S. (1996). A framework for the study of filial imprinting and the development of attachment. *Psychonomic Bulletin & Review*, *3*, 3–20.

Vergara, V., & Barrett-Lennard, L. G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals*, *34*, 123.

Vince, M. (1979). Postnatal effects of prenatal sound stimulation in the guinea pig. *Animal Behaviour*, *27*, 908–918.

Vince, M., Armitage, S., Walser, E., & Reader, M. (1982). Postnatal consequences of prenatal sound stimulation in sheep. *Behaviour, 81*, 128–139.