Post-Partum Whistle Production in Bottlenose Dolphins

Running Headline: Fripp and Tyack: Maternal Whistle Production in Dolphins

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Abstract

Despite much research on bottlenose dolphin signature whistles, few have investigated the role of maternal whistles in early calf development. We investigated maternal whistle use in the first weeks postpartum for captive dolphins. The overall whistling rate increased by a factor of ten when the calves were born and then decreased again in the third week of the one surviving calf. Adult whistles were distinguished from calf whistles based on the extent of frequency modulation and were further classified into signature and non-signature whistles by comparison to a dictionary of known whistles. The average rate of maternal signature whistle production increased significantly from 0.02 whistles per dolphin-minute before the calves were born to 0.2 and 0.3 whistles in weeks 1 and 2, decreasing again to 0.06 in week 3 for the mother of the surviving calf. Percent maternal signature whistles changed similarly. Signature whistle production by non-mothers did not change when the calves were born. A likely function of this increase in maternal signature whistle production is that it enables the calf to learn to identify the mother in the first weeks of life.

Keywords: bottlenose dolphin, *Tursiops truncatus*, vocal behavior, mother-infant, signature whistles, imprinting

When mammals approach parturition, their behavior changes in many ways. Bottlenose dolphins, *Tursiops truncatus*, for instance, spend more time alone just before giving birth and a great deal of time rubbing, nursing, and caring for their calf just afterwards (Fripp 1999, Mello and Amundin 2005). Dolphin mothers in Shark Bay, Australia also spend a significant amount of time in the calves' first weeks keeping them away from other dolphins (Mann and Smuts 1998). Previous research has suggested that whistle production may increase shortly before parturition (Mello and Amundin 2005). The current study was designed to investigate whistle production during the first weeks following parturition.

Signature whistles are individually-distinctive whistles where the unique frequency contour of each dolphin's whistle is highly stereotyped (Caldwell *et al.* 1990). Although dolphins can whistle at birth (Caldwell and Caldwell 1979), they are not born with a stereotyped signature whistle (Caldwell *et al.* 1990, Sayigh 1992), but develop a unique signature whistle by listening to the whistles in their environment (Fripp *et al.* 2005). Dolphin calves are also born swimming in a highly social environment. The opportunities for confusion when a calf wanders away from its mother abound. Dolphins in general, and mothers and calves in particular, are known to use signature whistles to keep in contact with each other when separated (Sayigh 1992, Smolker *et al*. 1993, Janik and Slater 1998). Since signature whistles are individually variable, a calf may have to learn to recognize its mother's whistle before it can find her again when separated. We predicted that the need for a calf to learn its mother's signature whistle might elicit an increase in maternal signature whistle production in the calf's first weeks.

To investigate post-partum whistle production, four pregnant dolphins in captivity were studied from shortly before to shortly after the births of their calves. Both their overall whistle production and their signature whistle production were quantified.

Methods

Data Collection

Whistles were recorded from four pregnant female bottlenose dolphins (*Tursiops truncatus*) and their newborn calves, as well as another mother (Sharky) and her seven-month-old female calf (Daphne), at the Kolmårdens Djurpark in Kolmården, Sweden (Table 1). All four newborn calves were male. Calf 1 was born in late April of 1995, and died at 7 days of age. Calves 2, 3, and 4 were born in succession in late May and early June. Calves 2 and 3 died at 9 and 10 days respectively. Calf 4 survived but spent one day (June 9: his 6th) in isolation for medical treatment. Recordings were started in March and continued through the end of Calf 4's third week (March 21 to June 24, Table 1). Sharky and Daphne were moved out of the pool shortly after Calf 1 was born. Similarly, Mother 1 was moved out shortly after Calf 2 was born, and Mother 3 was moved out on Calf 4's 6th day.

Ten-minute focal animal samples (Altmann 1974) were taken on each pregnant mother or newborn calf five times daily, at approximately 0900, 1030, 1330, 1600, and 1800 hours. The times were selected to represent all the contexts the dolphins experienced, including presence and absence of trainers and the public, feedings and shows. The breeding pool was closed to the public during the calves' first two weeks and no training was done (only feeding). Dolphins were observed from underwater viewing windows, and behavior was recorded on an IBM Thinkpad 755Cs with The Observer 3.0 (Noldus). Acoustic recordings were made from a single hydrophone placed in the corner of the pool near the observation station simultaneously with the behavioral observations. Acoustic recordings were made with a hydrophone from High Tech, Inc. and a Radio Design Labs STM2 preamplifier onto one channel of a Panasonic VHS, PAL-format, stereo VCR.

For each calf, focal samples were classified as Pre-Birth, Week 1, Week 2, Week 3, or Other (Table 1). Pre-Birth samples included all samples on the calf's mother taken in the 3 weeks before the calf was born. Week 1 included focal samples from that calf in the calf's first 7 days. Week 2 included samples in days 8 through 14, and Week 3 included samples in days 15 through 21. Only Calf 4 had samples taken in week 3. Calf 1 only had samples taken in week 1. Calves 2 and 3 had samples taken in weeks 1 and 2. Calf 4's Week 1 samples did not include samples from June 9, when Calf 4 was in acoustic isolation. Any samples that did not fit into one of those four categories were classified as "Other" and were not used to evaluate maternal whistle use. Some of these samples were used to evaluate the difference between calf and adult whistles (see "Separating Out Calf Whistles" below).

Whistles

A total of 4116 min were digitized from 412 focal samples (Table 1). Recordings were played back on a Samsung SV-300W VCR and filtered with a Frequency Devices 9002 programmable filter with a high-pass filter at 2 kHz and a post-filter gain of 5x. Sounds were digitized at 80 kHz onto an IBM PC with a Dalanco Spry model 250 Analog to Digital conversion board. Whistles were then extracted by an automatic extraction and sorting procedure (Fripp 1999). This procedure first extracted all sounds with energy above a pre-set noise threshold and then sorted the sounds by bandwidth. In this way, the sorting procedure separated the broadband burst-pulse sounds and echolocation clicks from the narrowband whistles. A human observer then checked the sound files to eliminate spurious detections. More than 200,000 cuts were made, yielding more than 23,000 whistles (Table 1).

Files containing whistles were separated into files with single whistles and files with two or more overlapping whistles. Overlapping whistles are whistles that occurred at the same time. While they could often be separated visually (one could see that there were multiple whistles), they could not be separated by the automatic contour extractor (see below). These whistles were therefore excluded from the contour-based analysis, but the number of whistles in these files was counted and added to the number of files containing single whistles to determine the total number of whistles collected. Overlapping whistles were only saved and counted from the May and June recordings (see Table 1).

After whistle extraction, the frequency contour of each whistle's fundamental frequency was extracted using the procedure described by Buck and Tyack (1993) (see Figure 1A). With this procedure, the contour is extracted by taking the frequency with the highest amplitude in each time-block of the spectrogram after noise compensation (Buck and Tyack 1993). Spectrograms were produced with an FFT size of 512 samples/block, a step size of 512, a Hamming window, a low frequency cutoff of 4 kHz, a high frequency cutoff of 22 kHz and a band-reject filter that excluded 15.05 to 16.05 kHz (to account for monitor noise). To avoid extracting harmonics and to be sure the contour represents the whistle's fundamental frequency, the extraction program looks for peaks at half and one-third the peak initially detected. Following extraction, contours were visually checked and only contours where the majority of the points fell on the whistle's visible fundamental were included (see Figure 1A). Contours with a few points off the visible fundamental were left as extracted. Correcting these points would have required significant massaging of the data (particularly in the case of Mother 1, who had actual silences in her whistle, see Figure 1A), which we considered inappropriate.

The following measures were calculated from the acoustic data: whistle rate per minute, whistle rate per dolphin-minute, average contour length (in ms), and percent of whistles overlapping other whistles. Whistle rate per dolphin-minute was calculated by dividing the whistle rate per minute by the number of dolphins in the group at the time to get an estimate of the average whistle rate per individual. For each measure, a value was calculated for each 10-minute sample. A mean was then calculated for each focal animal for each section (Pre-Birth, Week 1, Week 2, Week 3). All means are presented ± standard error. An ANOVA was performed using those means (one for each section for each focal). Analysis of signature whistle rate was performed in the same way (see below).

Separating Out Calf Whistles

Because we were interested in changes in the adult repertoire, but with a single hydrophone cannot determine repertoires of individual dolphins, we needed a way to separate calf whistles from the general pool of whistles. Caldwell and Caldwell (1979) described the whistles of newborn bottlenose dolphins as short, quavery, and lacking frequency modulation. This contrasts with the whistles of adult dolphins, which are narrow-band over short time periods and highly frequency modulated over the entire duration of most whistles (Caldwell *et al.* 1990). The Caldwells hypothesized that, using this information, it should be possible to distinguish calf whistles from those made by adults (Caldwell and Caldwell 1979). Following this hypothesis, we used our data to try to separate calf whistles from adult whistles by means of their frequency characteristics.

For this test, focal samples were classified into four categories: “Adult Only,” “Neonate Alone,” “No Neonate,” and “Adult + Neonate” (Table 1). The “Adult Only” whistles come from the week immediately before Calf 2 was born, when only four adult dolphins were in the group. The “Neonate Alone” whistles come from Calf 4 at 6-days old, when he was held in a separate pool and out of acoustic contact with any other dolphin. These two periods allowed us to look at known adult whistles and compare them to known calf whistles. During the other two periods there were mixed groups of adults and calves. The “No Neonate” period included the samples from March and the samples from the week before Calf 1 was born. During this time, there were five adult females (four pregnant) and one 7-month old calf in the pool (Table 1). The “Adult + Neonate” period includes all the time when newborn calves were in the pool. The contours from these mixed groups were classified secondarily, using the classification of the known adult and neonate whistles.

From the contours in these categories, the contour duration and several frequency parameters were calculated (with a custom program written in Matlab 6.5, Mathworks).

The frequency parameters were measured from the quartile contour, which is the contour with the lowest and highest 25% of the frequencies removed. This was done to remove outliers and noise spikes from the contour, which were significant in some contours. Noise spikes occur when the signal-to-noise ratio is unusually low in a particular time-bin of the spectrogram. Although some information was lost in this process, the use of the quartile contour prevented noisy contours from dominating the results. Six parameters were measured from the quartile contour: minimum frequency, maximum frequency, median frequency, frequency range, frequency asymmetry, and sweep rate. Frequency range is a measure of the overall frequencies used in the entire whistle, defined as (maximum frequency)-(minimum frequency). The frequency asymmetry is defined as (median-min)/(max-min). This measure will vary from 0 (median equals minimum) to 1 (median equals maximum) (see Fristrup and Watkins 1994). Sweep rate is a measure of frequency modulation, defined as range/duration.

Contours from the “Adult Only” and “Neonate Alone” categories were classified by these parameters using linear discriminant analysis (Systat 7.0, SPSS). The centroids of each group were then calculated, and Wilks’ λ was used to test the equality of the centroids. The contours from the two mixed groups, “No Neonate” and “Adult + Neonate,” were classified afterwards using the same discriminant function. To classify these cases, the Mahalanobis distance (defined as *(x-mean)/cov(x-mean)*) from each group mean was calculated for each case. The case was classified into the group whose mean was closer. If the contour was equidistant between groups, no classification decision was made. Later analysis of adult whistle use was done only on contours that were classified as adult by this analysis.

Signature Whistle Analysis

In addition to the overall repertoire, we wished to look at the specific changes in signature whistle use. The contours in all sections were therefore classified using dictionary contour comparison (DCC: Buck and Tyack 1993, Fripp *et al.* 2005). To perform DCC, a series of dictionary contours (DCs) are selected to represent the types of whistles generally encountered. All contours are then compared to these DCs using dynamic time warping (DTW), a procedure that correlates the frequencies of two contours after allowing non-linear warping in time (but not in frequency) of one contour to fit the other (Buck and Tyack 1993). The DTW algorithm does not calculate similarity for whistles that differ in duration by more than a factor of two, and assigns a similarity of 0 to those comparisons. Following the DTW, each contour was assigned to the DC with the greatest similarity, so long as that similarity was greater than a predetermined threshold (Fripp *et al.* 2005). If the contour did not have a similarity greater than the threshold with any DC, it was classified as not assigned to a DC. A comparison of methods has shown the combination of DCC and DTW to be a good method for separating known categories of whistles, such as signature whistles (Fripp 1999).

For this data set, DCs were selected to represent the signature whistles of all the dolphins in the group (not including the neonatal calves who did not yet have signature whistles). In addition, a few typical non-signature whistle contours were also included, identified as typical by cluster analysis of a random sample of whistles (see Fripp 2005). Signature whistles of the mothers were determined by other researchers, by isolating the mothers after the calves were grown, and are published elsewhere (Mello and Amundin

2005). We confirmed these whistles by comparing them to whistles recorded shortly after the calves produced bubblestreams. For each calf, one adult-like whistle consistently showed up among the whistles produced directly after a calf produced a bubblestream. In all cases, these whistles matched the contour of the calf's mother's signature whistle. Because we were recording with only one hydrophone, we had no means to individually identify the producer of any given whistle. Whistles were therefore chosen for the dictionary contours to represent the breadth of whistles heard from the group and the contours of the known signature whistles of the adults.

The entire group of DCs is shown in Figure 1B. The DCs included variants of the signature whistles with differing numbers of loops (which is typical, see Caldwell *et al.* 1990), because the DTW would consider similar whistles with different numbers of loops to be dissimilar. Unfortunately, the DTW could not distinguish the whistles of Mother 1 from those of Mother 3. However, the periods for Calf 1 and Calf 3 did not overlap at all (even the Pre-Birth days), and Mother 1 was removed from the pool a week before Calf 3 was born. Therefore, although Mother 3 could be augmenting Mother 1's whistle rate, it is unlikely that Mother 1 impacted Mother 3's rate. The analysis of the DCC classified contours as one of the following: Mother 1/Mother 3, Mother 2, Mother 4, Sharky, Daphne, Non-signature whistle (those contours listed in Figure 1 as "Unidentified"), or not assigned to a DC.

Results

Total Whistle Sample

The most striking change between the pre- and post-partum whistle use was that the rate of whistling increased by an order of magnitude when the calves were born, from 0.27 ± 0.45 whistles per dolphin-minute to 2.86 ± 0.39 (Figure 2A, ANOVA F(3,7)=9.8, P=0.007). The whistle rate remained high in Week 2 (3.26 ± 0.45) and then decreased again in Week 3 (0.80 ± 0.78). Bonferroni post-hoc tests showed that the Pre-Birth whistle rate was significantly lower than the whistle rate in Weeks 1 and 2 (P=0.02).

In addition, the whistles themselves changed. The contour length was significantly longer in Week 1 than in the Pre-Birth period, changing from 375 ± 43 ms to 632 ± 37 ms on average (Figure 2B, ANOVA F(3,7)=10.2, P=0.006). The contour length decreased again in Week 2 (to 523 ± 43 ms) and even more in Week 3 (to 272 ± 75 ms). Bonferroni tests showed that Week 1 was significantly different from Pre-Birth and Week 3 (P=0.02).

The percentage of whistles overlapping other whistles also increased, although this difference was not significant (Figure 2C, ANOVA F(3,7)=2.1, P=0.186). The percent overlap was 5% ± 7% in the Pre-Birth period, 23.5% ± 6% in Week 1, 26% ± 7% in Week 2, and 9% ± 12% in Week 3. This result may indicate a shift in the dolphins’ use of the whistles, although there was a great deal of variation between focal dolphins on this measure.

The rate of overlapping whistles, combined with the whistle rate and average duration, can be used to determine whether the whistles are randomly timed with respect to each other. To test this, whistles were randomly placed in a 600 second block of time (equivalent to 10 minutes, the duration of our samples) and the proportion of whistles that overlapped other whistles (i.e. were closer to another whistle than the average whistle duration) was calculated. For each section, the number and duration of whistles were set based on the observed values of whistle rate per minute (note that this is different from whistle rate per dolphin-minute) and average contour length (Table 2). A P-value was generated from the proportion of 10,000 simulations with a greater percentage of overlaps than the observed rate (Table 2). As expected, the overlap rate increased with the increase in number and duration of whistles (from 1% to 12% on average), but the simulated increase was not as great as the observed increase. The observed overlap rate from the Pre-Birth period was not significantly different from the simulated overlap rate (P=0.07, Table 2). The observed overlap rates from all three postpartum weeks were significantly higher than the simulated rates, however (P<0.005, Table 2). These results indicate that the whistles were randomly timed with respect to each other before the calves were born but were closer together than expected after the calves were born.

Separating Calf Whistles from Adult Whistles

There are two possible explanations for the changes in whistle rate and use discussed above, which are not mutually exclusive. One explanation is that newborn calves whistle a great deal. Because they are newborns, their whistles can be expected to be different from, and be used differently than, the adult whistles. The second explanation is that adults whistle more and differently in the weeks after calves are born.

To distinguish between these possibilities, adult and calf whistles need to be separated. Obviously, the best way to do this would be to study individual repertoires. However, with a single hydrophone, there is no way to determine which dolphin produced a given whistle. Other researchers have taken advantage of bubblestreams produced by dolphins to assign individual repertoires (e.g. McCowan and Reiss 1995), but recent research has shown that bubblestreams do not always provide a representative sample of a dolphin's whistle repertoire (Fripp 2005).

Previous researchers have suggested that the acoustic characteristics of the whistles could be used to separate adult whistles from calf whistles (Caldwell and Caldwell 1979, Caldwell *et al.* 1990). To determine whether it would be possible to separate neonatal whistles from adult whistles based on their acoustic characteristics, we compared the whistles recorded when only adults were in the pool (Calf 2's Pre-Birth week, see Table 1) to the whistles recorded from a 6-day old neonatal calf in acoustic isolation (Calf 4, see Methods).

Adult and Neonate Whistles

There were clear differences between the adult ("Adult Only") whistles and the neonate ("Neonate Alone") whistles (Figure 3). Neonate whistles were significantly longer than adult whistles on average (507 ± 15 ms *vs.* 426 ± 17 ms, t-test t(695)=-3.2, P<0.001), although the adults produced the longest whistles (7% of adult whistles were more than a second long, compared to none of the neonate whistles). Adult whistles had significantly higher quartile frequency ranges than neonate whistles (2.6 ± 0.1 kHz *vs.* 1.2 ± 0.05 kHz, t-test t(695)=-9.2, P<0.001). As discussed in the methods, the quartile frequency range is the bandwidth of the central 50% of the frequencies (in other words, with the lowest and highest quartiles of frequencies removed). For whistles with a great deal of frequency modulation, the quartile range will be quite a bit smaller than the apparent frequency range on the figure (e.g. Figure 3A). Adults also had significantly higher sweep rates (10.4 ± 0.7 Hz/ms *vs.* 4.6 ± 0.5 Hz/ms, t-test t(695)=-6.0, $P<0.001$). These results mean that the adult whistles had significantly greater frequency modulation than the neonate whistles, as expected.

The discriminant analysis successfully separated the adult whistles from the neonate whistles (Figure 3B). Overall, 79% of the known adult and neonate whistles were classified correctly (76% of adult, 87% of neonate). The discriminant functions relied primarily on the asymmetry and the sweep rate. The duration, frequency range, median frequency, and maximum frequency were also incorporated, although with smaller weights. The mean discriminant function score for adult whistles was –0.53, while for neonate whistles it was 0.978 (Wilks' $\lambda = 0.658$, $P<0.0001$).

Mixed Groups

The measurements of the whistles in the two mixed groups, “No Neonate” and “Adult + Neonate,” tended to resemble the adult whistles more than the neonatal whistles. However, the average duration of the “Adult + Neonate” whistles was extremely long (646 ± 3 ms), even compared to the “Neonate Alone” whistles. The sweep rate was correspondingly low (5.2 ± 0.1 Hz/ms), most likely the result of the very high durations. Unfortunately, whistles longer than one second were not diagnostic of adult whistles. Approximately 14% of the whistles in the mixed groups were longer than a second, with the long whistles divided between calf and adult whistles by the discriminant analysis. When the whistles from the two mixed groups were classified using the discriminant function determined above, the “No Neonate” contours were classified almost exactly the same as the “Adult Only” whistles: 79% adult and 21% neonate (Figure 3B). The “Adult + Neonate” whistles, on the other hand, appeared to be almost evenly split, with 49% adult and 51% neonate.

Whistle Rate of Adult Whistles

The whistle-rate and contour-length analysis was redone using only adult whistles as determined by the discriminant analysis described above. Average adult whistle rate per dolphin-minute increased in the same way that the overall whistle rate per dolphin-minute had (ANOVA F(3,7)=13.6, P=0.003; Pre-Birth different from Weeks 1 and 2 by Bonferroni post-hoc tests, P=0.01). The adult whistle rate per dolphin-minute is calculated based on the number of adults in the group, not the total number of dolphins. Average adult contour length also increased in the calves’ first weeks (ANOVA F(3,7)=4.8, P=0.041). These results indicate that the changes in overall whistle rate and use are at least partly due to changes in adult whistling patterns, rather than the whistling behavior of the newborn calves. Because the discriminant analysis relied on whistle contours, overlapping whistles could not be used in this analysis, as overlapping whistles confuse the contour extractor. An analysis of what proportion of overlapping whistles in this time period are calf vs. adult would be interesting, however, and is worthy of later investigation.

Whistle Rate of Calf Whistles

The whistle-rate and contour-length analyses were also redone using only calf whistles as determined by the discriminant analysis of the whistles in the calves' first three weeks. As with adult whistles, the rate of calf whistles per dolphin-minute was calculated based on the number of calves, not the total number of dolphins. The average rate of calf whistles per dolphin-minute was 3.0 ± 0.5 in Week 1, 2.6 ± 0.5 in Week 2 and 1.0 ± 0.9 in Week 3. However, this change was not significant, possibly because of the small sample size (total N = 8 focal-week pairs, ANOVA F(2,5)=2.0, P=0.23). The average calf contour length also started high and then fell, from 620 ± 80 ms in Week 1 to 552 ± 92 ms in Week 2 to 261 ± 160 ms in Week 3, but again, the change was not significant (ANOVA F(2,5)=2.0, P=0.23). These results indicate that some aspects of the changes in overall whistle rate and use in the calves' first weeks are also due to changes in calf whistling patterns.

Dictionary Contour Comparisons

To categorize whistles by type, all contours were compared to a dictionary of typical contours (Figure 1). Overall, the dictionary contour comparison (DCC) classified 58% of the contours as dictionary contour non-signature whistles and 20% as dictionary contour signature whistles (Table 3). 22% of the contours did not match any of the dictionary contours. Of the contours that were previously classified as "calf" whistles by the discriminant analysis, 90% were non-signature whistles, 9% could not be classified, and only 1% was (incorrectly) classified as signature whistles. These last were all classified as matching Mother 4's signature whistle, which is somewhat similar to non-signature whistle upsweeps that are common among dolphins (see Table 3, Figure 1). Adult whistles were classified as 39% signature whistles, 26% non-signature whistle, and 35% other. The eight contours that were not classified as adult or calf by the discriminant analysis were all similarly not classified by the DCC.

Signature Whistle Use

Maternal Signature Whistles

Adult signature whistle use was investigated using only those contours that were classified both as adult by the discriminant analysis and as a signature whistle by the DCC. The production of signature whistles by each mother was considered relative to the birth of her calf; we classified her signature whistles by the periods described in the methods: Pre-Birth, Week 1, Week 2, and Week 3.

The change in maternal signature whistle production was investigated using three measures: the average rate of maternal signature whistles/dolphin-minute, maternal signature whistles as a percent of the total adult whistles, and maternal signature whistles as a percent of the total signature whistles (Figure 4). The average rate of maternal signature whistling increased significantly from the Pre-Birth period to the first few weeks of the calves' lives (ANOVA P=0.005, Figure 4A). Interestingly, the highest rate of signature whistles occurred during Week 2; Week 1 was intermediate between Pre-Birth and Week 2. The rate of signature whistling decreased again in Week 3 for Mother 4. Maternal signature whistles also increased as a percent of both the total adult whistles and the adult signature whistles (ANOVA F(3,8)=5.2 P=0.03 and F(3,8)=6.1 P=0.02,

Figure 4B and C). In both cases, the greatest proportion of maternal signature whistles occurred in Week 1, and the proportions declined steadily in Weeks 2 and 3.

Signature Whistle Use by Non-Mothers

To determine whether the change in whistle production was confined to mothers, the signature whistle use of other dolphins was investigated over the same periods. Because of the sequential nature of the births, signature whistle use by non-mothers could only be tested in the Pre-Birth vs. Week 1 periods for certain combinations of calves and dolphins (Table 4). Non-neonates (adults and 7-month old Daphne) had to be in the pool for both the Pre-Birth period and at least some portion of the calf's first week. Adults could not be caring for a neonate during either period. Because the whistles of Mother 1 and Mother 3 could not be distinguished, neither could be used for the other's calf. Analysis of this data set showed that the dolphins did not change their rate of signature whistle production when calves that were not their own were born (paired t-test t(6)=1.4, P=0.21, see Table 4). This result is consistent with the increase in maternal signature whistles as a percent of the total signature whistles heard (Figure 4C).

Calf 4's Unusual First Week

Calf 4 had a rather unusual first week, which merits a separate discussion. This calf was born approximately a week after Calf 2 died. As soon as Calf 4 was born, before Mother 4 could turn around to find him, Mother 2 took him with her to the surface. Calf 4 remained with Mother 2 until his 6th day, when he was removed from the pool for medical treatment. When he was returned to the group later that day, Mother 2 ignored him and Mother 4 reclaimed him. He remained with Mother 4 until weaning.

These unusual circumstances allow us to look at postpartum signature whistle use with respect to whether or not the mother is actually caring for a calf (Figure 5). Mother 4's signature whistle rate was high on day 1 (during much of which Mother 4 was in labor) and again starting on day 7 (Figure 5). On the days when Mother 4 was not caring for her calf, her signature whistle rate decreased again. This indicates that for Mother 4, increased signature whistling was related to actually caring for her calf. Her signature whistle rate increased when she began caring for the calf again, on day 7. In fact, her signature whistle rate on day 7 was unusually high, higher than any of the other mothers on any day of their calves' lives (0.7 whistles/dolphin-min *vs.* max = Mother 3 d9, 0.64; average max = 0.35). Although there was some variability (esp. an unusually high whistle rate for both adults on day 13, see Figure 5), for the most part Mother 4's signature whistle rate decreased slowly over the calf's next two weeks.

Interestingly, Mother 2 did not increase her signature whistle rate when she was caring for Calf 4 (Figure 5). This may have indicated that she was treating Calf 4 as if he was Calf 2, who would have been two weeks old. Based on Mother 4's behavior, two weeks may be beyond the time when the mothers are increasing their signature whistle production. Alternatively, she could have considered caring for Calf 4 somehow different from caring for her own calf and therefore behaved differently. However, a separate analysis was done of the dolphins' non-vocal behavior, including time as nearest neighbor, nursing, affiliative contact such as rubbing, and retrieving which is a maternal behavior (Fripp 1999). Mother 2's non-vocal behavior toward Calf 4 was equivalent to the maternal behavior she showed to her own calf (Fripp 1999).

Discussion

In this study, dolphin mothers produced more signature whistles in the first week of their calves' lives than they had previously. By the third week of the calf's life, the only mother of a surviving calf had returned to her previous rates of signature whistle production. Only mothers changed their rate of signature whistle production after their own calf was born: dolphins did not change their rate of signature whistle production when calves were born to other dolphins.

Many things change when calves are born and changes in vocal behavior are to be expected. Mothers, and other dolphins, might be expected to produce more or different whistles when swimming with newborn calves than when swimming only with adults. Previous work has recorded changes in adult whistling behavior shortly after calves are born (e.g. Sayigh 1992, Mello and Amundin 2005), but the exact nature of these changes was not clear. One hypothesis is that the mother could be using her signature whistle to communicate with the other adults. In that case, however, one would predict that all the dolphins would increase their signature whistle rate, not just the mother. Probably the most obvious hypothesis is that the increase in only maternal signature whistle production could be explained by the need for a mother to keep in contact with her calf. Signature whistles are known to be used for this purpose (Sayigh 1992). However, the decrease in signature whistle production by Mother 4 in week 3 does not fit that hypothesis, as calves actually wander further from their mothers as they get older (Mann and Smuts 1998). If the result that mothers do not keep up their increased signature whistle production represents a general trend, another hypothesis is necessary.

Alternative Hypothesis I: Imprinting

Mann and Smuts (1998) suggested another hypothesis that may help explain this pattern. They found that dolphin mothers (*Tursiops sp.*) in Shark Bay, Australia do not allow their newborns to spend time alone with other dolphins, although they do tolerate non-social separations. The mothers' intolerance of social separations changes to tolerance in the calf's second week. Mann and Smuts (1998) hypothesized that this shift reflects a period of imprinting during which calves learn to recognize their mothers' signature whistles.

Bottlenose dolphins are highly social, living in a fission-fusion society where a calf will encounter many other dolphins before it is weaned (Wells 2003). The combination of precocious locomotion (i.e. the ability to swim at birth) and sociality is associated with imprinting in other species (Hess 1959). A calf can easily get separated from its mother and find itself among many other dolphins. Imprinting allows young animals to learn to recognize their mothers quickly and avoid confusion.

Mann and Smuts' (1998) imprinting hypothesis predicts an increase in maternal signature whistle production in the first week of a calf's life. This increase should be followed by a decline shortly after mothers begin tolerating social separations. High rates of signature whistles may continue for a short time to reinforce the learning, but once learning has occurred, the mother should produce fewer signature whistles. Signature whistle production by other animals in the group should not change during this time.

Our results show a clear increase in maternal signature whistle production without a corresponding increase in non-maternal signature whistle production. These results support the imprinting hypothesis: our interpretation is that bottlenose dolphin calves imprint on their mothers' signature whistles in the first week of their lives, and their mothers facilitate this process by producing their signature whistles at higher than normal rates for the calves to learn. The results from Mother 4 suggest that the mothers are decreasing their signature whistle production again in week 3, which is predicted by the imprinting hypothesis of Mann and Smuts (1998). Unfortunately, with only one calf surviving to week 3, and a calf with an unusual first week at that, this evidence is not particularly strong. Future work to determine whether most mothers decrease their signature whistle production in week 2 or 3 is necessary to truly test this hypothesis.

Learning to Recognize your Mother

Vocal recognition between mothers and infants has been seen in other species of mammals, especially species of pinnipeds and bats (e.g. McCulloch and Boness 2000, Balcombe and McCracken 1992). In most of these cases, however, it is primarily the mother who recognizes the calls of the infants, not the other way around (McCulloch and Boness 2000), although in some species the recognition is mutual (Trillmich 1981; Gisiner and Schusterman 1991, Balcombe and McCracken 1992, Insley 2001).

The phenomenon of imprinting as a specialized learning mechanism whereby infants learn to recognize their mothers was first described in birds (Lorenz 1937). Early discussions of imprinting described it as a fairly rigid phenomenon, occurring primarily in birds, characterized by a constrained sensitive period, and irreversible (Lorenz 1937).

Since then, imprinting has been described in other taxa, including a number of ungulates, which are related to dolphins, and other mammalian species (e.g. Hess 1959, Altmann 1963, Alcock 1998, Thewissen *et al.* 2001). Imprinting by infants appears to be more common in species that are highly social and those with precocious locomotion (Hess 1959). Dolphins fit both patterns (Wells 2003).

In some bird species, the critical period for imprinting is as short as a few hours (Lorenz 1937). In some mammals, the critical period for imprinting is the first few weeks of life (e.g. days 5-14 for the shrew, Alcock 1998). The one-to-two week critical period suggested by Mann and Smuts (1998) is therefore in line with durations reported for other mammalian species. In addition, ungulates sometimes hide with their young until imprinting is complete (e.g. Hersher *et al.* 1963a). The dolphin mothers' intolerance of social separations (Mann and Smuts 1998) may reflect a similar process. Since Lorenz's time, additional evidence has also shown the sensitive period of imprinting is often more flexible than originally thought (Hersher *et al.* 1963b).

In his discussion of imprinting, Lorenz (1937) comments that the irreversibility of the process is what sets imprinting apart from other types of associative learning. It is not yet clear how irreversible the process of learning a mother's signature whistle is in dolphins. However, an investigation of previous evidence in bottlenose dolphins may illuminate this question. The theft, or attempted theft, of newborn dolphins, as occurred with Calf 4, has been reported previously (e.g. Dudok van Heel and Meyer 1974, Prescott 1977, Shallenberger and Kang 1977, Thurman and Williams 1986, Mann and Smuts 1998). Most interestingly, these incidents almost always occur in the first day of the calf's life. If the imprinting hypothesis holds, this may indicate that after the calf has imprinted on its mother, such theft is much more difficult. The fear of such theft may drive the maternal intolerance of early social separations (Mann and Smuts 1998). The shift to tolerance at the end of the first week might then be explained by the completion of a relatively irreversible imprinting process.

The theft and subsequent return of Calf 4 may also illuminate the flexibility of the imprinting process. Mann and Smuts (1998) reported a shift in maternal tolerance of social separations starting as early as days 4 to 7. In this study, however, maternal signature whistle production remained high through the second week (days 8 to 14). Mother 4's increased signature whistle production after Calf 4 returned to her and through his second week may indicate that the critical period can last as long as two weeks, although that length of time is not always necessary. The constant exposure to other dolphins that a calf experiences in captivity may also necessitate a longer period of exposure to the mother's whistle than would be required in the wild, or possibly by a lone mother-calf pair in captivity. Flexibility in imprinting critical periods has been reported for other species as well (Bateson 1979, Hersher *et al.* 1963b).

Alternative Hypothesis II: Modeling Signature Whistles for Male Calves

A second alternative hypothesis is raised by the observation that all four of these calves were male. Dolphin signature whistles develop over the course of the calf's first year of life, and the contour of the signature whistle is learned from the whistles the calf hears in its first few months (Sayigh *et al.* 1990, Fripp *et al.* 2005). Previous research has shown that male calves are more likely than female calves to develop signature whistles similar to their mothers' signature whistles (Sayigh *et al.* 1995). An increase in maternal signature whistle production with a male calf may therefore be related to the mother using her signature whistle as a model for the son's future signature whistle. The short-lived nature of the increase, potentially demonstrated here by Mother 4, could indicate that the most important time for learning one's future signature whistle is the first few weeks. An early period of learning for a vocalization that only appears later is well known from studies of birdsong (e.g. Marler 1970, Kroodsma and Pickert 1984). However, the exposure to song needed for young birds is not so early or so short-lived. Most birds are exposed to song tutoring for their entire time in the nest and often some of their fledgling stage (Marler 1970, Kroodsma and Pickert 1984). One might expect, therefore, that tutoring of male dolphins would continue for longer than two to three weeks, especially considering how much longer dolphin calves are dependent on their mothers (3 to 5 years, Wells 2003).

The fact that the current study was done in captivity is an argument against this hypothesis however. Sayigh's work showed that while free-ranging males were more likely to have signature whistles similar to their mothers, captive-born males were not (Sayigh 1992). However, if the mothers' behavior has an innate basis, they may produce more signature whistles for their male calves regardless of the situation. Therefore, while being in captivity is an argument against this hypothesis, it is not strong evidence to discount this hypothesis. Future work investigating maternal signature whistle use with female calves is the best way to answer this question. This hypothesis predicts that mothers should only increase their signature whistle production with male calves and not with females.

Caveats

Certain methodological issues must be addressed when discussing these results. Dolphins are known to mimic each other's signature whistles (Tyack 1986). To classify the whistles, we matched the contours to the known contours of the dolphins' signature whistles. We therefore could not distinguish between maternal signature whistle production and mimicry of the mother's signature whistle by other dolphins. However, at most, signature whistle mimicry has been reported to account for 25% of the signature whistles recorded (Tyack 1986). The increase in maternal signature whistle use was far greater than 25%. However, a short-lived increase in signature whistle mimicry related to the novelty of the new calf cannot be discounted here. An investigation of individual whistle use is needed to distinguish that hypothesis but awaits the advent of new technology to allow us to assign whistles to individuals (see Fripp 2005 for a discussion of this problem).

We must also consider the deaths of three of the four calves. Data for week 3 were only available for one calf, and this calf had a very unusual first week. His mother also showed the highest whistle rate of all the mothers, raising the concern that she may be dominating the results. Re-analysis of the results shows that not to be the case. The other three mothers increased their signature whistle production in the first two weeks of their calves lives as well ($F(2,5)=6.9$, $P=0.04$ without Mother 4), and their signature whistles comprised a greater proportion of all the signature whistles produced during the calves first two weeks ($F(2,5)=8.0$, $P=0.03$ without Mother 4). Because only the one calf survived to week 3, we can only see the week 3 decrease from that calf's mother. However, Mother 2's behavior while caring for Calf 4 (not increasing her signature whistle rate) also suggests a decrease in signature whistle use as a calf grows older. Alloparenting, taking care of other animals' infants, is often seen among postpartum females (Hrdy 1977, McBride & Kritzler 1951, Riedman & Le Boeuf 1982). Several researchers have suggested that these females are hormonally "primed" to respond to young infants (Hrdy 1977, Riedman & Le Boeuf 1982). The recent loss of Calf 2 may have primed Mother 2 to respond when Calf 4 was born. She therefore may have been treating Calf 4 as if he were Calf 2. If the whistling behavior of mothers is also hormonally primed by the timing of birth, then Mother 2 may have been beyond the typical period of high whistle rates.

Another issue that needs to be addressed is the DCC's confusion of Mother 1's whistles with Mother 3's. As was stated before, Mother 1 was moved out a week before Calf 3 was born. The increase in production of Mother 1/Mother 3 whistles in Calf 3's first weeks is therefore attributable to Mother 3, not Mother 1. Signature whistles produced by Mother 3 could have contributed to the increase in Mother 1 signature whistles following Calf 1's birth. However, no other dolphin increased her signature whistle production following the birth of another dolphin's calf (note that that analysis did not include Mother 3 at Calf 1's birth). It is therefore unlikely that Mother 3 would have changed her signature whistle production when Calf 1 was born.

The final methodological issue that needs to be addressed is the fact that this work was done in captivity. It is possible that these results are an artifact of life in captivity where animals are in constant acoustic contact with each other. It is possible that the only way to differentiate the mother in this environment is through high whistle rates. However, this hypothesis would not predict a decrease in whistling when the calf is only three weeks old. Additionally, changes in adult whistling behavior shortly after calves are born have been recorded in the wild as well (Sayigh 1992). Although animals are not is as constant acoustic contact with each other in the wild, there are many other dolphins around and many opportunities for a calf to be lost in the wild. We would therefore expect that a calf would have a similar, if not greater, need to recognize its mother as it has in captivity.

Separation of Calf and Adult Whistles

In the current study, the extent of frequency modulation could be used to distinguish neonate whistles from adult whistles by discriminant analysis, as predicted by Caldwell and Caldwell (1979). Although the discriminant analysis classified the majority of the known whistles properly, 24% of the “known adult” whistles were classified as neonatal. One possible reason for this is the connection between the pools at Kolmårdens Djurpark. Although Daphne, the seven-month-old calf, had been moved into another pool, that pool was not acoustically isolated from the study pool. Whistles from that calf may have been heard in the study pool even when only adults were physically present in the study pool. This is a likely explanation for why the “Adult Only” and “No Neonate” categories appear so similar. It is important to note, however, that the whistles from the “Neonate Alone” category come from a pool that was acoustically isolated from the rest of the facility. All the whistles in that category were produced by the single calf in that pool.

The discriminant analysis indicated that the “Adult + Neonate” contours were approximately half adult and half neonate. That result is interesting considering that on most days there was only one neonate in a group of two to four adults. This may indicate that the neonates were far more vocal than the adults. Alternatively, the adults may have been imitating the neonatal sounds, although this seems unlikely. More likely, some of the whistles classified as neonate in this context were misclassified. Since 24% of the "Adult Only" whistles were classified as neonate (and 13% of the "Neonate Alone" whistles were classified as adult), we should expect some of the mixed whistles to be misclassified. Additionally, the postpartum increase in duration may be partly due to an increase in the number of loops in the adult whistles. As noted in the results, this could cause a corresponding decrease in the sweep rate, which could cause the whistle to be misclassified, as sweep rate was one of the major parameters used by the discriminant analysis.

Our results indicate that adult whistles change depending on context (pre- vs. post-partum), as do previous results (Janik *et al.* 1994, Janik and Slater 1998). Since all the known neonate whistles in this sample were from a single calf in a particular context, alone with no adults in visual or acoustic contact, contextual changes in calf whistles may have impacted our results as well. A follow-up study investigating the differences in the whistles used by adults and calves in different contexts would be therefore useful. However, the current study demonstrates a method whereby unidentified whistles can be classified as probably produced by an adult or a young calf. This ability should aid in the understanding of bottlenose dolphin vocal and behavioral development.

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Literature Cited

ALCOCK, J. 1998. Animal Behavior. Sinauer Associates, Sunderland, MA.

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

ALTMANN, M. 1963. Naturalistic studies of maternal care in moose and elk. Pages 233-253 *in* H.L. Rheingold, ed. Maternal Behavior in Mammals. John Wiley and Sons, New York, NY.

BALCOMBE, J.P. AND G.F. MCCRACKEN. 1992. Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? Animal Behaviour 43:79-87.

BATESON, P. 1979. How do sensitive periods arise and what are they for? Animal Behaviour, 27:470-486.

BUCK, J.R. AND P.L. TYACK. 1993. A quantitative measure of similarity for *Tursiops truncatus* signature whistles. Journal of the Acoustical Society of America 94:2497-2506.

CALDWELL, M.C. AND D.K. CALDWELL. 1979. The whistle of the Atlantic bottlenose dolphin (*Tursiops truncatus*) - ontogeny. Pages 369-401 *in* H.E. Winn and B.L. Olla, eds. Behavior of Marine Animals, Vol. 3 Cetaceans. Plenum Press, New York, NY.

CALDWELL, M.C., D.K. CALDWELL AND P.L. TYACK. 1990. Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. Pages 199-234 *in* by S. Leatherwood and R.R. Reeves, eds. The Bottlenose Dolphin. Academic Press, New York, NY.

DUDOK VAN HEEL, W.H. AND M.M. MEYER. 1974. Birth in dolphins (*Tursiops truncatus*, Mont.) in the Dolphinarium Harderwijk, Netherlands. Aquatic Mammals 2:11-22.

FRIPP, D.R. 1999. Techniques for studying vocal learning in bottlenose dolphins, *Tursiops truncatus*. Ph.D. Dissertation, Woods Hole Oceanographic Institution/Massachusetts Institute of Technology.

FRIPP, D.R. 2005. Bubblestream-whistles are not representative of a bottlenose dolphin's vocal repertoire. Marine Mammal Science 21:29-44.

FRIPP, D.R., C. OWEN, E. QUINTANA-RIZZO, A. SHAPIRO, K. BUCKSTAFF, K. JANKOWSKI, R. WELLS, AND P. TYACK. 2005. Bottlenose dolphin calves appear to model their signature whistles on the whistles of community members. Animal Cognition 8:17-26.

FRISTRUP, K.M. AND W.A. WATKINS. 1994. Marine Animal Sound Classification. Woods Hole Oceanographic Institution Technical Report No. 94-13, Woods Hole, MA.

GISINER, R. AND R.J. SCHUSTERMAN. 1991. California sea lion pups play an active role in reunions with their mothers. Animal Behaviour 41:364-366.

HERSHER, L., J.B. RICHMOND AND A.U. MOORE. 1963a. Maternal behavior in sheep and goats. Pages 203-232 *in* H.L. Rheingold, ed. Maternal Behavior in Mammals. John Wiley and Sons, New York, NY.

HERSHER, L., J.B. RICHMOND AND A.U. MOORE. 1963b. Modifiability of the critical period for the development of maternal behavior in sheep and goats. Behaviour 20:311-320.

HESS, E.H. 1959. Imprinting. Science 130: 133-141.

HRDY, S.B. 1977. The Langurs of Abu. Harvard University Press, Cambridge, MA.

INSLEY, S.J. 2001. Mother-offspring vocal recognition in northern fur seals in mutual but asymmetrical. Animal Behavior 61:129-137.

JANIK, V.M. , G. DEHNHARDT AND D. TODT. 1994. Signature whistle variations in a bottlenose dolphin, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 35:243-248.

JANIK, V.M. AND P.J.B. SLATER. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56:829-838.

KROODSMA, D.E. AND R. PICKERT. 1984 Sensitive phases for song learning: effects of social interaction and individual variation. Animal Behavior 32:389-394.

LORENZ, K. 1937. The companion in the bird's world. Auk 54:245-273.

MANN, J. AND B.B. SMUTS. 1998. Natal attraction: kidnapping, allocare, and separations among wild Bottlenose dolphin (*Tursiops truncatus*) mothers and infants. Animal Behaviour 55:1097-1113.

MARLER, P. 1970. A comparative approach to vocal learning: song development in white-crowned sparrows. Journal of Comparative Physiology and Psychology 71:1-25.

MCBRIDE, A.F. AND H. KRITZLER. 1951. Observations of pregnancy, parturition, and postnatal behaviour in the bottlenose dolphin. Journal of Mammology 32:251-265.

MCCOWAN, B. AND D. REISS. 1995. Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): role of learning. Journal of Comparative Psychology 109:242-260.

MCCULLOCH, S., AND D.J. BONESS. 2000. Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. Journal of Zoology (London) 251:449-455.

MELLO, I. AND M. AMUNDIN. 2005. Whistle production pre- and post-partum in bottlenose dolphins (*Tursiops truncatus*) in human care. Aquatic Mammals 31: 169-175.

PRESCOTT, J.H. 1977. Comments on captive births of *Tursiops truncatus* at Marineland of the Pacific (1957-1972). Pages 71-76 *in* S.H. Ridgway and K. Benirschke, eds. Breeding Dolphins: Present Status, Suggestions for the Future. Report No. MMC-76/07 to the US Marine Mammal Commission, Washington, DC.

RIEDMAN, M.L. AND B.J. LE BOEUF. 1982. Mother-pup separation and adoption in Northern elephant seals. Behavioral Ecology and Sociobiology 11:203-215.

SAYIGH, L.S. 1992. Development and functions of signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus.* Ph.D. Dissertation, MIT/WHOI Joint Program, WHOI 92-37.

SAYIGH, L.S., P.L. TYACK, R.S. WELLS, AND M.D. SCOTT. 1990. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behavioral Ecology and Sociobiology 26:247-260.

SAYIGH, L.S., P.L. TYACK, R.S. WELLS, M.D. SCOTT, AND A.B. IRVINE. 1995. Sex differences in whistle production in free-ranging bottlenose dolphins, *Tursiops truncatus.* Behavioral Ecology and Sociobiology 36:171-177.

SHALLENBERGER, E.W. AND I. KANG. 1977. Dolphin births at Sea Life Park. Pages 77-84 *in* S.H. Ridgway and K. Benirschke, eds. Breeding Dolphins: Present Status, Suggestions for the Future. Report No. MMC-76/07 to the US Marine Mammal Commission, Washington, DC.

Smolker, R. A., J. Mann and B.B. Smuts. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. Behavioral Ecology and Sociobiology 33:393-402.

Thewissen, J.G.M., E.M. Williams, L.J. Roe, and S.T. Hussain. 2001. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. Nature 413: 277-281.

Thurman, G.D. and M.C. Williams. 1986. Neonatal mortality in two Indian Ocean bottlenose dolphins bred in captivity. Aquatic Mammals 12:83-86.

Trillmich, F. 1981. Mutual mother–pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21–42.

Tyack, P.L. 1986. Whistle repertoires of two bottlenose dolphins, *Tursiops truncatus*: Mimicry of signature whistles? Behavioral Ecology and Sociobiology 18:251-257.

Wells, R.S. 2003. Lessons from long-term study and life history. Pages 32-56 *in* F.B.M de Waal and P.L. Tyack, eds. Animal Social Complexity: Intelligence, Culture, and Individualized Societies. Harvard University Press, Cambridge, MA.

Tables

Table 1: Periods with different calves during which whistles were sampled.

Dates (1995)	10’ Focal Samples	Whistles	Mother 1 and Calf 1[a]	Mother 2 and Calf 2[a]	Mother 3 and Calf 3[a]	Mother 4 and Calf 4[a]	Sharky and Daphne[b]	Discrim Analysis Period
March 21 - 29	80	> 1,138[c]	*Other*	*Other*	*Other*	*Other*	Present	No Neonate
April 18, 24	32	> 330[d]	Pre-Birth	*Other*	*Other*	*Other*	Present	No Neonate
April 25, 28, 29	52[e]	> 524[d]	Week 1	*Other*	*Other*	*Other*	Present 1st day	Adult + Neonate
May 16, 18, 20, 21	60	636	*Other*	Pre-Birth	Pre-Birth	Pre-Birth	Not Present	Adult Only
May 22, 24, 28	45	3,465	Present 1st day	Week 1	Pre-Birth	Pre-Birth	Not Present	Adult + Neonate
May 29	15	2,862	Not Present	Week 2	Pre-Birth	Pre-Birth	Not Present	Adult + Neonate
May 30; June 1, 2	40	6,439	Not Present	*Other*	Week 1	Pre-Birth	Not Present	Adult + Neonate
June 4	15	1,810	Not Present	*Other*	Week 1	Week 1	Not Present	Adult + Neonate
June 6, 8	30	3,757	Not Present	*Other*	Week 2	Week 1	Not Present	Adult + Neonate
June 9	4	250						Neonate Alone
June 10	5	519	Not Present	*Other*	Not Present	Week 1	Not Present	Adult + Neonate
June 12, 14, 16, 18	19	1,244	Not Present	*Other*	Not Present	Week 2	Not Present	Adult + Neonate
June 20, 22, 24	15	360	Not Present	*Other*	Not Present	Week 3	Not Present	Adult + Neonate
33 recording days	412	23,334						

[a] Sections for each calf only include focal samples on that calf or that calf’s mother.

[b] Daphne was seven months old and therefore was not a subject of this study. Sharky is her mother.

[c] Not all the whistles from this section were saved, due to computer error.

[d] Not all the overlapping whistles from these sections were saved, due to computer error.

[e] One sample during this period was cut short (by 4.25’) due to equipment failure, so only 515.75’ were recorded from these 52 samples.

Table 2: Results of Randomization Trials for Whistle Overlaps

	Input Numbers			Results			
Section	Whistles	Length	% Overlap	Mean	Range	> Observed	P-value
Pre-Birth	11	375 ms	5%	0.6%	0-18%	670 (6.7%)	0.07
Week 1	125	631 ms	23%	12.2%	4-24%	2 (0.02%)	0.0002
Week 2	94	523 ms	26%	7.7%	0-21%	0 (0.0%)	0.000
Week 3	24	272 ms	9%	1.0%	0-17%	21 (0.2%)	0.002

Table 3: Dictionary Contour Comparisons

	Type of Dictionary Contour:			
Whistle Type*	Signature Whistle	Non-Signature Whistle	None	Total
Adult	39% (2,935)	26% (1,989)	35% (2,594)	100% (7,518)
Calf	1% (69)	90% (6,564)	9% (691)	100% (7,324)
No Decision	0%	0%	100% (8)	100% (8)
Overall	20% (3,004)	58% (8,553)	22% (3,293)	100% (14,850)

*Whistle type determined by discriminant analysis (see “Separating Calf Whistles from Adult Whistles”).

Table 4: Non-Maternal Signature Whistles per Dolphin-Minute

Calf	Signature whistle Type	Pre-Birth Rate*	Week 1 Rate*
Calf 1	Mother 2	0.01	0.00
	Mother 4	0.00	0.00
	Sharky	0.00	0.01
	Daphne	0.00	0.00
Calf 2	Mother 1/Mother 3	0.02	0.12
	Mother 4	0.02	0.01
Calf 3	Mother 4	0.02	0.07
Average		0.01	0.03

*Pre-Birth and Week 1 rates were **not** significantly different by paired t-test (t(6)=1.4, P=0.21). N=7 dolphin-calf pairs, with a total of 377 whistles, averaging 54 whistles/dolphin-calf pair.

Figure Legends

Figure 1: Contours

A. Sample Spectrograms and Contours. Spectrograms and matching contours of two of the whistles used to make dictionary contours from the signature whistles of Mother 1 and Mother 3.

B. Dictionary Contours. The contours used as dictionary contours for the dictionary contour comparison. The labeled contours include variants of the signature whistle from each dolphin. “Unidentified” contours were typical whistles but could not be identified as the signature whistle of a specific dolphin. Note that the analysis of the dictionary contours could not distinguish Mother 1 from Mother 3.

Figure 2. Whistle Count Analysis for May and June. For each plot, each bar represents the average of the three focals, each focal having been averaged over all the focal samples from that mother-calf pair, when the calf was living. These plots include all whistles except contour length, which includes only usable contours.

A. Average whistles/dolphin-minute. ANOVA, F(3,7)=9.8, P = 0.007; Bonferroni post hoc tests show that Pre-Birth is significantly different from Weeks 1 and 2.

B. Average contour length. ANOVA, F(3,7)=10.2, P = 0.006; Bonferroni post hoc tests show that Week 1 is significantly different from Pre-Birth and Week 3.

C. Percent Overlaps. ANOVA, F(3,7)=2.1, P = 0.186.

Figure 3. Separating Adult and Calf Whistles.

A. Sample Contours

Adult Only: Examples of whistles from the week immediately before Calf 2 was born, when four adult females were in the group. These were classified as “Adult” by the discriminant analysis.

Neonate Alone: Examples of whistles produced by a 6-day-old male, Calf 4, acoustically isolated from the rest of the group. These were classified as “Calf” by the discriminant analysis.

B. Discriminant Analysis Separating Adult and Calf Whistles; Discriminant analysis was done using “Adult Only” and “Neonate Alone” categories, with a 79% accuracy rate. “No Neonate” and “Adult + Neonate” sections were then classified based on the previous discriminant analysis.

Figure 4: Maternal Signature Whistle Use. For each plot, each bar represents the average of the four focal dolphins, each focal having been averaged over all the focal samples on that mother-calf pair, when the calf was living. These plots include only usable contours that have been classified as adult by the discriminant analysis and as maternal signature whistles by the dictionary contour comparisons.

A. Average maternal signature whistles/dolphin-minute. ANOVA, F(3,8)=9.4, P = 0.005; Bonferroni post hoc tests show that Pre-Birth is significantly different from Week 2.

B. Maternal signature whistles as a percent of all adult whistles. ANOVA, F(3,8)=5.2, P=0.028; Bonferroni post hoc tests show that Pre-Birth is significantly different from Week 1.

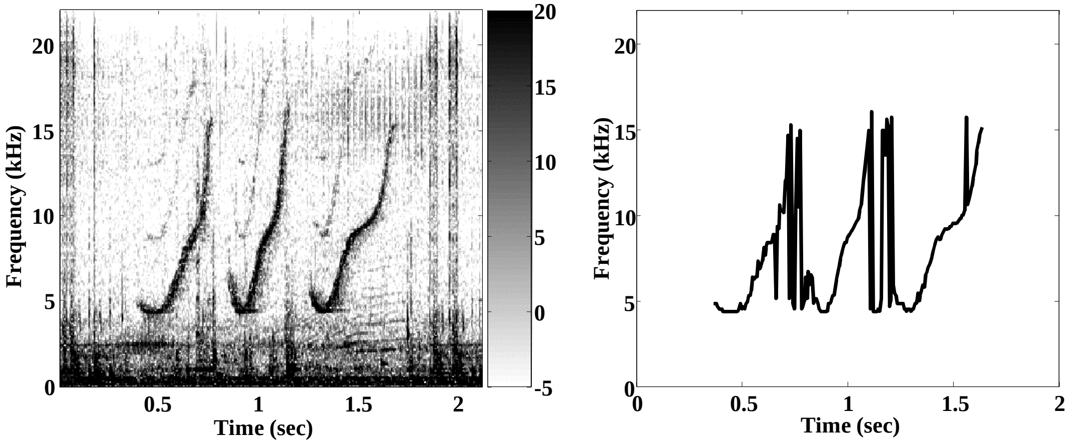
C. Maternal signature whistles as a percent of all signature whistles. ANOVA, F(3,8)=6.1, P=0.019; Bonferroni post hoc tests show that Pre-Birth is significantly different from Week 1.

Figure 5: Signature Whistle Use in Calf 4’s First Week: Average signature whistles/dolphin-minute. Each point represents the average for that mother of all the Calf 4 focal samples on that day. Only usable contours that were classified as adult by the discriminant analysis and as signature whistles by the dictionary contour comparisons have been included. Mother 2 stole Calf 4 from Mother 4 at birth and returned him on day 6.

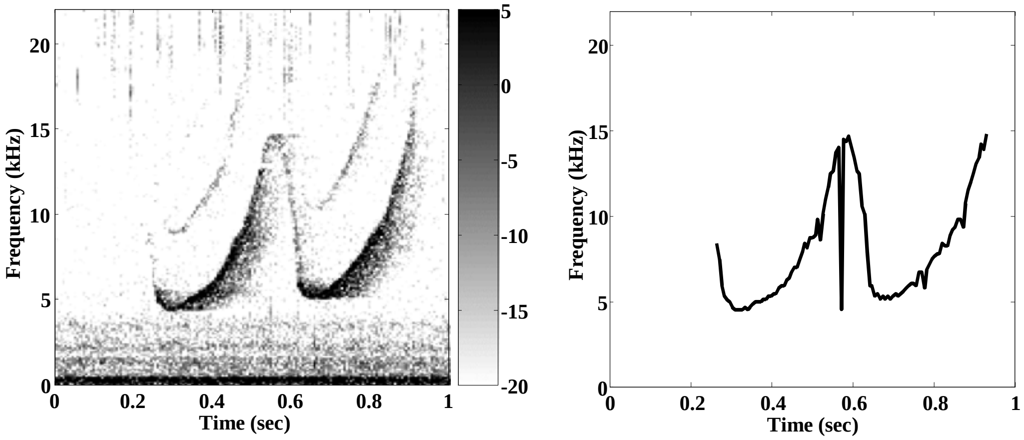
Figure 1: Contours

A. Sample Spectrograms and Contours.

Mother 1



Mother 3



B. Dictionary Contours.

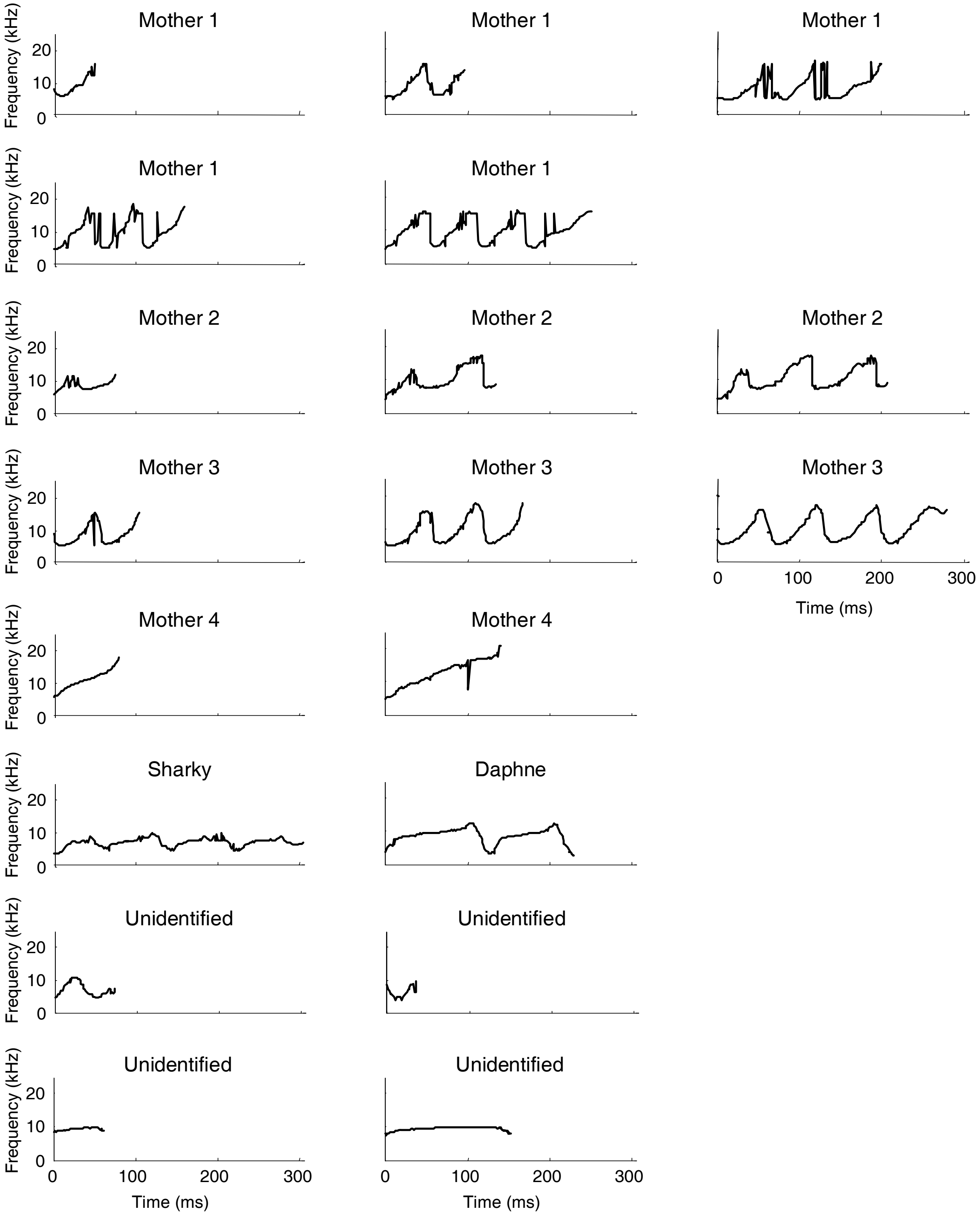
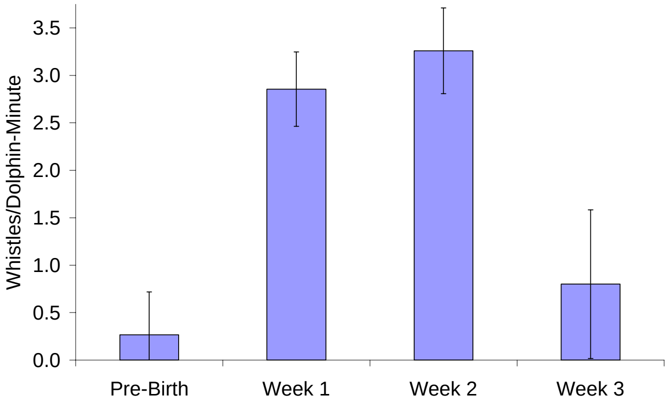
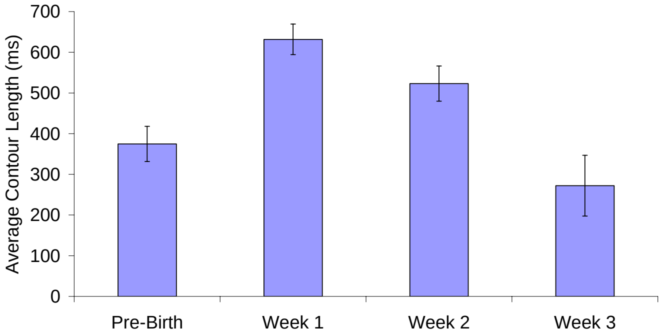


Figure 2

A. Average whistles/dolphin-minute



B. Average contour length.



C. Percent Overlaps.

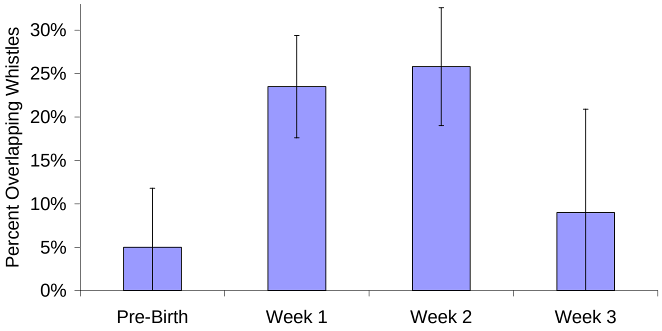
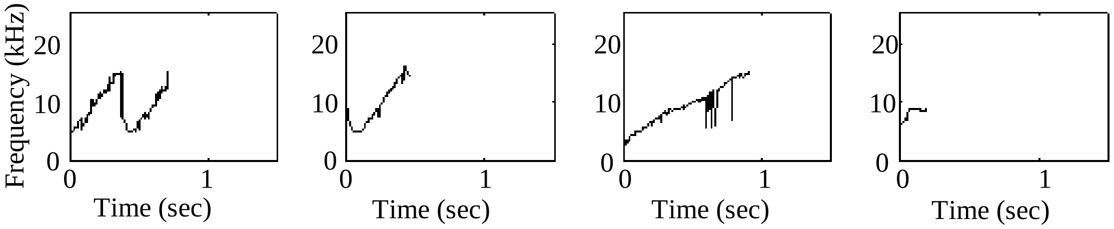


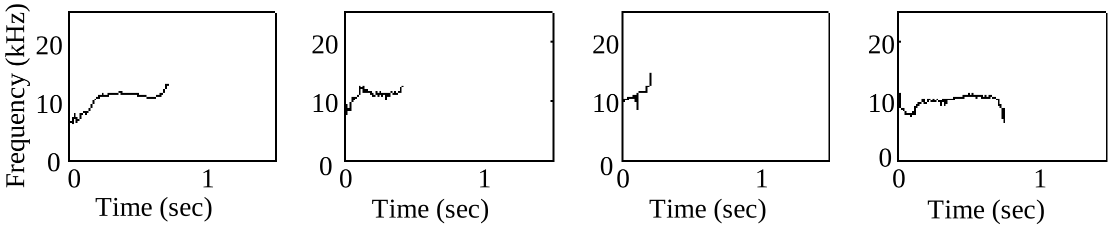
Figure 3. Separating Adult and Calf Whistles.

A. Sample Contours

Adult Only:



Neonate Alone:



B. Discriminant Analysis Separating Adult and Calf Whistles

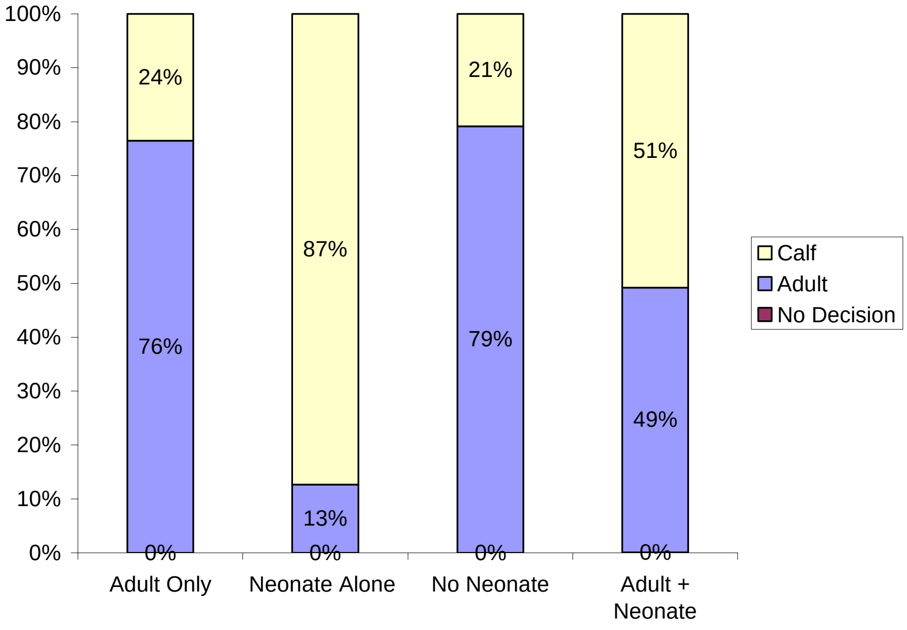
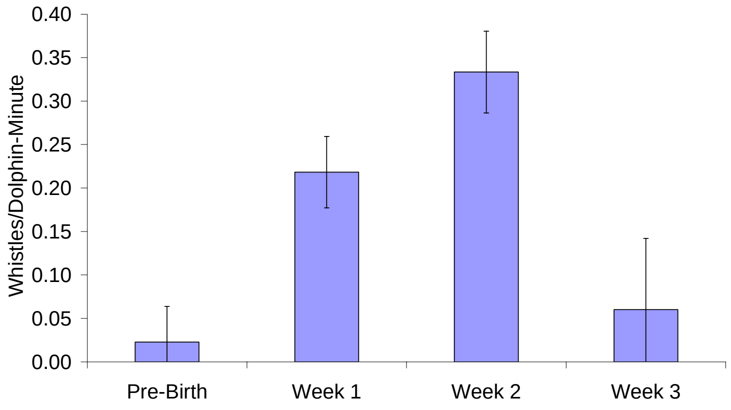
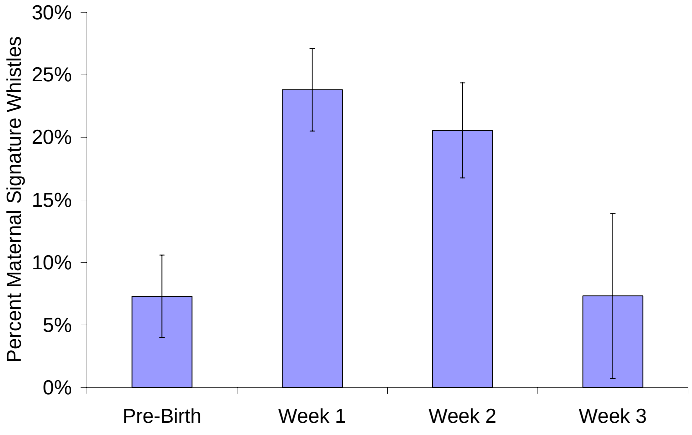


Figure 4: Maternal Signature Whistle Use.

A. Average maternal signature whistles/dolphin-minute.



B. Maternal signature whistles as a percent of all adult whistles.



C. Maternal signature whistles as a percent of all signature whistles.

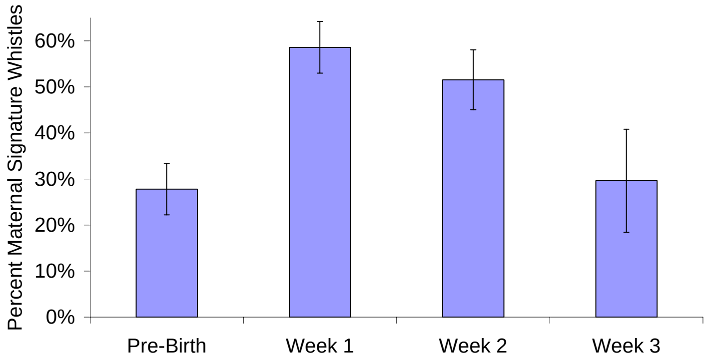


Figure 5: Signature Whistle Use in Calf 4's First Week: Average signature whistles/dolphin-minute.